4

Earthworms, Plants, and Soils

Renée-Claire Le Bayon[1], Géraldine Bullinger[2], Andreas Schomburg[1], Pascal Turberg[3], Philip Brunner[4], Rodolphe Schlaepfer[3], and Claire Guenat[3]

ABSTRACT

The importance of engineers is increasingly recognized in soil science because of their implication in most important pedological processes. Furthermore, they contribute to ecological functions provided by soils in both natural and human-modified environments. In this review, we focus on the role of two ecosystem engineers: (1) plants, their root system, and associated microorganisms and (2) earthworms. First, we explain why they are considered as major soil engineers, and which variables (texture, porosity, nutrient, and moisture dynamics) control their activities in space and time (hotspots and hot moments). Then, their roles in three processes of soil formation are reviewed, namely, rock and mineral weathering, soil structure (formation, stabilization, and disintegration), and bioturbation. For each of them, the involved mechanisms that occur at different spatial scales (from local to landscape) are presented. On one hand, tree uprooting plays a key role in rock weathering and soil profile bioturbation. In addition, living and dead roots also contribute to rock alteration and aggregation. On the other hand, earthworms are mainly involved in the formation of aggregates and burrows through their bioturbation activities and to a less extent in weathering processes. The long-term effects of such mechanisms on soil heterogeneity, soil development, and pathways of pedogenesis are discussed. Finally, we show how these two main ecosystem engineers contribute to provisioning and regulating services. Through their physical activities of burrowing and soil aggregation, earthworms and plants increase plant productivity, water infiltration, and climate warming mitigation. They act as catalysts and provide, transform, and translocate organic matter and nutrients throughout the soil profile. Finally, due to inter- and intraspecific interactions and/or symbiosis with microorganisms (arbuscular fungi, bacteria), they enhance soil fertility, decrease parasitic action, and bioremediate some pollutants. Future research is, however, still needed for a better understanding of the relationships between adequate soil management, agricultural practices, and soil biota in a perspective of relevant maintenance and durability of ecological services.

4.1. PLANTS AND EARTHWORMS ARE ECOSYSTEM ENGINEERS

4.1.1. Why Are Plants and Earthworms Called Ecosystem Engineers?

Ecosystem functioning and stability mainly depend on living organisms (biocenosis) being in equilibrium with their abiotic environment (biotope). The higher

---

[1] *Laboratory of Functional Ecology, Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland*

[2] *Institute of Construction and Environmental Technology, Haute école d'ingénierie et d'architecture, Fribourg, Switzerland*

[3] *Laboratory of Ecological Systems, ECOS & WSL, Ecole Polytechnique Fédérale, Lausanne, Switzerland*

[4] *Center for Hydrogeology and Geothermics, CHYN, University of Neuchâtel, Neuchâtel, Switzerland*

Hydrogeology, Chemical Weathering, and Soil Formation, Geophysical Monograph 257, First Edition.
Edited by Allen Hunt, Markus Egli, and Boris Faybishenko.

DOI: 10.1002/9781119563952.ch4

biodiversity is, the greater are resistance and resilience of ecosystems facing disturbances. Organisms themselves affect their own habitat through their activities and then modulate species richness and heterogeneity of the environment, and thus the ecosystem functions at several spatiotemporal scales. Such ecological interactions are usually distinguished in (1) trophic relationships encountered in ecological networks such as food webs (Ings et al., 2009) and (2) nontrophic relationships implying organisms that affect others by creating, modifying, maintaining, or destroying habitats, called "ecosystem engineers" (C. G. Jones et al., 1997, 1994; Wright & Jones, 2006). Independently from their origin and their location, ecosystem engineers initiate habitat formation in the abiotic environment, therefore creating a modified structural state. Environmental heterogeneity is then enhanced with new ecological niche opportunities and increased biodiversity (C. G. Jones et al., 2010). Moreover, ecosystem engineers contribute not only to structural changes but also to abiotic and biotic changes, processes that are interdependent with feedback effects (C. G. Jones et al., 2010). Allogenic engineers thus modify living or non-living materials from one state to another, whereas autogenic engineers modify their own structure and morphology; some engineers are both allogenic and autogenic at the same time (Berke et al., 2010; C. G. Jones et al., 1994, 1997).

Focusing on terrestrial ecosystems, soils play a central role in major global biogeochemical cycles and host the largest diversity of organisms (Smith et al., 2015). Among these organisms, plants and invertebrates are key components of soil genesis, functions, and properties, and their occurrence in the pedon is crucial, focusing on their engineering activities. This is particularly the case in the so-called "humipedon," the upper soil layers enriched in organic matter (mainly O and A) that experience interactions between vegetation and soil (Zanella et al., 2018). The activity of soil organisms is particularly high in humipedons and is strongly involved in organic matter recycling and provisioning, as well as the formation of biogenic structures such as burrows and aggregates. Earthworms and plant roots are particularly involved in these processes that result in aggregates of different size, shape, and water stability. They act mainly as allogenic engineers and are responsible for physical modifications but may also be involved in biological and biochemical processes (see sections 4.1.2 and 4.1.3). Plants and earthworms also share common features regarding their engineering activities. For instance, both contribute to aggregate and burrow formation, especially in the top 30 cm of soil. In temperate ecosystems, they are thus the main soil engineers creating habitats for other organisms, such as small arthropods like springtails or mites (Cameron et al., 2013; Eisenhauer, 2010; Liu et al., 2013).

Both plants and earthworms produce also chemical substances: exudates (Bais et al., 2006) and mucus, respectively (Salmon, 2001), which are enriched in water, carbon (C), and nitrogen (N). These secretions are major drivers of bacterial diversity and activities (Wu et al., 2017) and contribute to enhanced enzymatic activities (Gianfreda, 2015; Le Bayon & Binet, 2006) but also modulate the attraction of small arthropods (Salmon, 2001). Plant roots interact with earthworms, and their concomitant activity increases aggregate stability (Fonte et al., 2012; Schomburg, Schilling, et al., 2018; Schomburg, Verrecchia, et al., 2018).

4.1.2. Relationships Between Selected Soil Properties, Plants, and Earthworms

4.1.2.1. Soil texture

Texture is one of the main soil properties driving the general behavior of ecosystem engineers. For plants, the optimum spatial distribution of roots depends mainly on soil water and nutrients, whose retention is largely influenced by soil texture. Higher clay fractions promote retention of water and sorption of nutrients, whereas a high sand content tends to enhance drainage (Weil & Brady, 2017). On the other hand, high clay contents can lead to soil compaction and prevent root development, or even access of water, whereas sharp sand grains may cause abrasion of fine root tips (Coleman et al., 2004). Lipiec et al. (2016) showed that rough sand increases the tortuosity of wheat roots and decreases root length, diameter, and even root dry weight. Whereas most cultivated plants require soil with balanced proportions of silt, sand, and clay, some plants tolerate more severe constraints, such as shrubs living in desert or coastal dunes, where sand is predominant. In northern California, a native shrub (*Ericameria ericoides*) is well adapted to its sandy environment by developing an efficient root network that helps to retain coarse organic matter and decreases aeolian erosion. In a coastal dune system, shrub species (*Lupinus chamissonis* and *Ericameria ericoides*) serve also as ecosystem engineers acting at multiple levels of biological organization through both positive and negative effects on richness and biomass of herbaceous plants (Cushmann et al., 2010). *Phalaris arundinacea* is also well known to grow up in alluvial sandy soils. This pioneer herbaceous species is especially resistant to drought conditions and has an efficient root system that protects riverbanks from erosion (Schomburg, Schilling, et al., 2018). In these alluvial ecosystems with regular erosion and/or deposits of sediments during flood events, riparian trees act both as allogenic and autogenic engineers. By trapping sand and organic matter, they can modulate soil moisture and accelerate landform formation, particularly island growth (Gurnell & Petts, 2006).

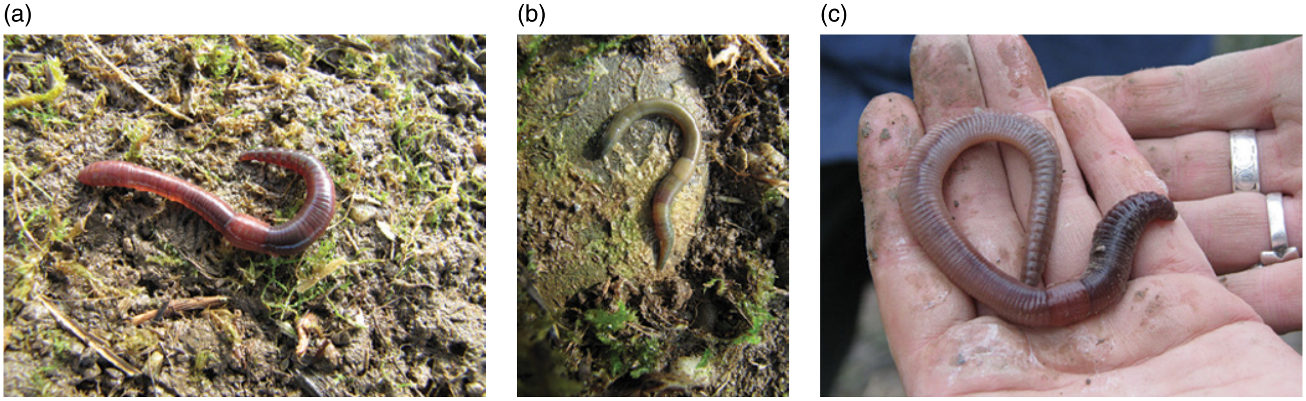

Figure 4.1 Ecological categories of earthworms. (a) Epigeic species, *Lumbricus rubellus*. (b) Endogeic species, *Allolobophora chlorotica* (c) Anecic species, *Lumbricus terrestris* (sometimes also classified as epi-anecic). Photos a and b, Claire Le Bayon; photo c, Géraldine Bullinger.

Soil texture also directly influences pedofauna. Indeed, soil macrofauna need material to construct biogenic structures (Bardgett, 2005; Coleman et al., 2004; Edwards & Bohlen, 1996; Lavelle et al., 1997, 2016), and through their selective choice of building components they often create gradients of organic and mineral particles in their living space (Edwards, 2004; Frouz et al., 2003; Jouquet et al., 2014, 2018; Véle et al., 2011). Earthworms select mainly both fine organic and mineral particles that they ingest and usually avoid soils with a high proportion of sand due to potential skin damages (Blouin, Hodson, et al., 2013; Blouin, Sery, et al., 2013; Curry & Schmidt, 2007; Lee, 1985). However, earthworms may also select sand grains that improve the grinding of leaf litter in their muscular gizzard (Marhan & Scheu, 2005; Schulmann & Tiunov, 1999). Depending on their ecological category, epigeic, endogeic, or anecic species as defined by Bouché (1977), earthworms differ in their habitat, not only in relation to soil depth but also to texture distribution in the soil profile.

Epigeics (Figure 4.1a) usually live in holorganic humus layers, dead wood, or composts, consuming and digesting organic matter without mixing it with mineral particles. They increase organic matter decomposition rates and act as ecosystem engineers by strongly affecting other litter-inhabiting organisms such as microfauna and microorganisms (Edwards, 2004). Endogeic species (Figure 4.1b) are mostly located in the shallow part of the soil and feed on soil and associated organic matter. To satisfy their dietary requirements, they actively move into the soil profile and build up long and dense horizontal branching burrows filled with their casts (Edwards & Bohlen, 1996). Endogeics prefer silty-clay soils, and their burrows and casts serve both as nutrient and habitat resources for plant roots (Lee, 1985). Anecic earthworms (Figure 4.1c) dig large vertical burrows that may extend several meters into the soil profile and thus prefer deep soils with fine texture (Bullinger-Weber et al., 2012; Salomé et al., 2011). These worms are especially efficient at burying fresh organic matter into their burrows using the strong muscles of their prostomium. By doing this, they largely contribute to the incorporation and the storage of organic materials in the subsoil. Through their bioturbation activity, and like endogeics, anecic earthworms excrete casts inside their permanent burrows, lining their walls with C-enriched mineral-organic material, but they may also seal their burrow openings with surface casts (middens). All these biogenic structures (burrows, casts, and middens) may serve as habitats for plant roots (and vice versa, as previously mentioned), but also for microfauna (springtails, mites, enchytraeids) and microorganisms (Eisenhauer, 2010). Besides these three ecological categories of earthworms, intermediate situations exist as epi-endogeic (*Lumbricus rubellus*) or endo-anecic ones (*Aporrectodea longa*), increasing the complexity of their role as ecosystem engineers.

4.1.2.2. Soil porosity

Soil porosity is the ratio between the volume of pores and the total soil volume. This porosity depends on several factors, including the size, shape, and arrangement of primary particles, as well as their cementing (Nimmo, 2004). Both burrowing by soil-dwelling animals and expansion of the root network create the largest biopores in soil. Soil aggregates also contribute to generating spaces into the soil; the intimate mixing of organic matter and mineral particles occurs either in the digestive system of animals, in particular earthworms, or by enmeshment of soil particles by roots, hyphae, and their exudates (Coleman et al., 2004; Milleret, Le Bayon, & Gobat, 2009; Milleret, LeBayon, Lamy, et al., 2009; Six et al., 2002; Tisdall & Oades, 1982). Consequently, vegetation and earthworms largely contribute to forming porosity in the humipedon, where their activities prevail.

Roots influence the soil pore system, but they are controlled by both soil and root characteristics. Bodner et al. (2014) showed that coarse root systems increase macroporosity by 30%, whereas plants with dense, fine root systems heterogenize the pore space and increase microporosity. Therefore, not only plants but also their lifetimes (perennial versus annual) influence the formation and the permanence of root systems (Yunusa & Newton, 2003). After root decay, which varies according to plant communities, several size classes of biopores are freed up, becoming then available for air and water transport (Bodner et al., 2014; Horn & Smucker, 2005; Mitchell et al., 1995).

Earthworms are well known to enhance porosity as they move through the soil, thus decreasing soil density (Johnson-Maynard et al., 2007) and improving soil aeration (Edwards & Bohlen, 1996) and water infiltration (Capowiez et al., 2014; Shipitalo & Le Bayon, 2004). The number of burrows, as well as their length, diameter, and above all their connectivity, are essential to ensure an efficient hydraulic conductivity (Johnson-Maynard et al., 2002; Pérès et al., 2010). The amount of organic matter, the diet type of the worms, and the soil texture are the main components that drive length and branching of earthworm burrows (Amossé, Le Bayon, et al., 2015; Amossé, Turlberg, et al., 2015; Lavelle & Spain, 2001). These burrow systems then depend on soil features but also on earthworm species that construct burrows of different length, diameter, and branching (Amossé, Le Bayon, et al., 2015; Amossé, Turlberg, et al., 2015; Bastardie et al., 2005; Capowiez et al., 2014). Moreover, Felten and Emmerling (2009) showed that species interactions may occur between anecic and endogeic earthworms. For instance, the burrowing activity of the endogeic *Octolasion tyrtaeum* is significantly reduced in the presence of the anecic *Lumbricus terrestris* compared to the specific single treatment, revealing potential interspecific competition and trophic niche separation (Felten & Emmerling, 2009).

4.1.2.3. Soil nutrient balance

In the vicinity of roots. The soil directly in contact with roots (i.e., the rhizosphere, see section 1.3) has very different physical, chemical, and biological properties compared with the bulk soil. Through their multiple activities of ecosystem engineering, plants create a gradient of soil water content and nutrient availability around their root system (Gilad et al., 2007; Guttierez & Jones, 2006). Moreover, carbohydrates formed by photosynthesis are transferred into rhizospheric soil where they stimulate microbial activity; in turn, microbial enzymes decompose soil organic matter, thus releasing nutrients through priming effects (Bengtson et al., 2012; Finzi et al., 2015). Huang et al. (2014) showed that plant exudates modulate fungal and bacterial activities, which also influence root exudation. Consequences on soil nutrient balances are obvious, and Finzi et al. (2015) showed that root-accelerated mineralization and priming effect can account for up to one third of the total C and N mineralized in temperate forest soils. As most of the plants have symbiotic relationships, arbuscular mycorrhizal fungi also contribute to nutrient availability by facilitating interplant nutrient transfer (Le Bayon & Milleret, 2009; Wilson et al., 2006). Mimmo et al. (2018) focused on how chemical, biochemical, and physical interactions occurring in the rhizosphere affect nutrient availability. They showed that qualitative and quantitative composition of root exudates depends on many factors (plant species, plant age, environmental conditions, etc.) and influences the mobilization of nutrients.

In casts and burrows. The selective ingestion of organic material contributes to the concentration of organic matter in casts compared to the surrounding soil (Edwards & Bohlen, 1996; Le Bayon et al., 2017; Lee, 1985; van Groenigen et al., 2019). The addition of mucus during the gut transit stimulates microorganisms and consequently enzyme activities, which enhance organic matter mineralization (Blouin, Hodson, et al., 2013; Chapuis-Lardy et al., 2011; Shipitalo & Le Bayon, 2004). A meta-analysis on cast fertility (van Groenigen et al., 2019) highlighted that nutrient availability is higher in casts than in bulk soil (total elemental concentrations increased by 241% and 84% for mineral N and available P, respectively). In addition, pH, cation exchange capacity, and base saturation are also increased. Earthworm burrow linings are also enriched in organic matter and nutrients compared to non-ingested soil (Jégou et al., 1998). Mucus, composed mainly of water, C, and N, serves as a lubricant to improve the displacement of earthworms. This resource enrichment leads to the presence of specific and active communities of microflora and microfauna directly located in the burrow walls (Jégou et al., 1998; Savin et al., 2004; Tiunov & Scheu, 1999), and enzyme activities are enhanced over 2–3 mm all along the linings (Le Bayon & Binet, 2006). Consequently, casts and burrows are major sources of bio-avaiblable nutrients that could directly be absorbed by plant roots (Milleret, Le Bayon, & Gobat, 2009; Hoang et al., 2016). As an example, roots of *Achillea millefolium* preferentially occupy burrows of the anecic *Lumbricus terrestris* (Cameron et al., 2014). Moreover, earthworm burrows provide interconnected channels that make easier the penetration of roots into the soil and serve as a regeneration niche for plants in grassland ecosystems (Milcu et al., 2006).

4.1.3. Hotspots, Hot Moments in the Soil: Rhizosphere and Drilosphere

The soil biota modulates physical, chemical, and biological properties of soils in several ways (Blouin, Hodson, et al., 2013; Coleman et al., 2004; Lavelle et al., 1997). Five areas in the soil with specific properties were thus defined by Beare et al. (1995): (1) the rhizosphere in the vicinity of plant roots, (2) the detritusphere in the organic layers, (3) the aggregatusphere encompassing soil aggregates, (4) the porosphere considering voids, and finally (5) the drilosphere, e.g. the soil under the influence of earthworms. Such "hotspots" of intense biological activity, also called "hotspheres," may represent more than 90% of the total biological activity concentrated in less than 10% of the total soil volume (Beare et al., 1995). Kuzyakov and Blagodatskaya (2015) underlined that hotspots located in rhizosphere and drilosphere can be associated with "hot moments" defined as short-term events or sequences of events inducing accelerated process rates, as compared to average rates. Hot moments induce successions in microbial communities and intense intra- and interspecific competition, thus affecting C use efficiency, microbial growth, and turnover. Consequently, the intensification of fluxes increases and such hot moments result in priming effects localized in microbial hotspots (Kuzyakov & Blagodatskaya, 2015).

4.1.3.1. Rhizosphere

The rhizosphere is the soil volume that interacts directly and immediately with living plant roots, from nanometers to centimeters in radial distance from the root surface (Richter et al., 2007). Organisms found in the rhizosphere include bacteria, fungi, nematodes, protozoa, algae, and microarthropods (Lynch, 1990; Raaijmakers et al., 2009). This diversity is mainly due to rhizodeposits released by plant roots, and these deposits are the main food source for microorganisms that modulate population density and activities of other organisms. Rhizodeposition is a mixture of several compounds such as lysis products of root cells, insoluble mucilages, soluble root exudates, and volatile organic C (D. L. Jones et al., 2009). Soil microorganisms are chemotactically attracted to these spots enriched in C and tend to proliferate in this particular environment (Lugtenberg & Kamilova, 2009). In return, microbial activity in the rhizosphere is essential for plant functioning, as it assists plants in nutrients uptake and offers protection against pathogen attack (Berendsen et al., 2012; see section 4.3.2). Therefore, the rhizosphere is a zone of communication between soil microorganisms and roots that occurs and changes continuously due to nutrient solubility, soil transport, or plant uptake (Mimmo et al., 2018). Huang et al. (2014) reviewed interactions between plants and rhizosphere microbes, focusing on how root exudates are involved in these processes. Regarding soil structure at a smaller scale, Foster (1998) and Bruand et al. (1996) showed the importance of bacteria and roots in rearranging and stabilizing soil properties. Feeney et al. (2006) discovered that soil microbes and plant roots modify their habitats by changing size and clustering properties (i.e. spatial correlation) of soil pores. Consequently, the rhizosphere is not only a hotspot of biochemical processes and fluxes but also a hotspot and a hot moment regarding aggregate formation.

4.1.3.2. Drilosphere

The drilosphere is the part of soil the influenced by earthworm burrowing and casting activities (Blouin, Hodson, et al., 2013; Johnson-Maynard & Strawn, 2016). Earthworm burrows, surface casts, and casts produced within the soil profile belong to the drilosphere, but also earthworm gut contents, as well as symbionts (Ojha & Devkota, 2014). Hence, the drilosphere displays a high degree of relationship between microorganisms and micro-, meso-, and macroinvertebrates. Generally, anecics and endogeics are involved in the drilosphere formation due to their ecological behavior and selective ingestion of particles (Curry & Schmidt, 2007). The permanent burrow system of anecic species (about 2 to 3 m depth) is an important network of root growth activity and microbial dispersal, while endogeic species are more located around the rhizospheric region (Hirth et al., 1998). As a consequence, soil biogeochemical properties within the drilosphere differ from those of the bulk soil, similar to the rhizosphere (Lipiec et al., 2016). Linking drilosphere and rhizosphere functioning is then obvious. Earthworms enhance plant growth and plant quality (van Groenigen et al., 2014) that is closely linked to drilosphere-rhizosphere interactions. Kim et al. (2017) also showed that some combinations of earthworm-mediated soil aeration, modification of moisture conditions in the rhizosphere and drilosphere, and comminution of organic matter modify microbial communities and significantly affect the N cycle.

4.2. PLANTS AND EARTHWORMS ARE IMPLIED IN SOIL FORMATION

Among biota, plants and earthworms mainly contribute to pedogenetic processes as ecosystems engineers. According to Blum et al. (2018), pedogenesis is defined as "the processes of formation and development of soils, resulting in many different soil bodies. Soils with common particular characteristics form a distinctive soil group or soil type or soil unit." Processes of soil formation are subdivided into two main groups: transformation and translocation. Transformation (weathering and formation of new minerals, decomposition and stabilization of organic matter, development of soil structure, ion exchange and redox processes, etc.) operates *in situ* and may involve some movement of substances over a very short distance (microns to millimeters). Translocation processes (transport of salts, organic and mineral substances, turbation, etc.) lead to displacement, sorting and mixing of solid matter within the soil profile (centimeters to meters). Both transformation and translocation are controlled by five main factors: climate, parental material, relief, biota, and time, resulting in the development of distinctive soil horizons with particular properties. These soil-forming factors determine both direction (pathways) and speed of pedogenesis.

In this section, we analyze the role of biota, in particular plants and earthworms, in key transformation and translocation processes during pedogenesis, namely, weathering of rocks and minerals, structure formation, and bioturbation. Although these processes can occur simultaneously and interact with each other, they are presented successively to facilitate understanding. In addition, for each process, the main impacts of earthworms, plants, roots, and their associated microorganisms are discussed. Nevertheless, the interactions between these two ecosystem engineers are not detailed.

4.2.1. Rock and Mineral Weathering

Weathering is a process involving both the breakdown of rocks and minerals and the formation of new secondary products. This cascade process creates continuous changes in the environment and gathers physical or mechanical disintegration, but also chemical alteration. The contribution of soil organisms is widely recognized, but it is difficult to disentangle the effects of purely mechanical from chemical weathering because they frequently act synergistically.

4.2.1.1. Plants

4.2.1.1.1. Mechanical weathering. Mechanical weathering is mainly due to root growth in length and girth, which causes axial and radial pressures during rock penetration. Swelling of roots, promoted by water absorption, can exert a huge pressure, slowly splitting a rock apart (Gabet et al., 2003). Fine roots penetrate joints and fractures of rocks, widen them, and contribute to the conversion of bedrock to regolith (fractured soil parental material), or to deepening/thickening regolith. However, the efficiency of this mechanism remains unclear because the tensile strength of most unweathered rock exceeds the pressure that growing roots can reach. Pawlik et al. (2016) reported that maximum radial pressures of root growth range from 0.51 to 0.9 MPa, while the tensile strength of crustal rocks ranges from 1 to 25 MPa. Tree uprooting also contributes to rock weathering and soil formation at different spatial scales, from landscape to fine scales such as pits and mounds (Šamonil, Král, et al., 2010; Šamonil, Tejnecký, et al., 2010). Mechanical and biochemical weathering processes are also closely linked because when roots have entered rocks, moisture fluxes along roots are then modified, and physiological functions of plants (respiration, nutrition, transpiration) immediately induce chemical weathering. Roots subsequently play a role of transmission pathways for moisture, nutrients, microorganisms, and heat. There is also an indirect input of water, organic matter, and bioconstructions in places presently or previously occupied by roots (Pawlik et al., 2016).

4.2.1.1.2. Chemical weathering. Soil organisms (lichens, mosses, plants, fungi, bacteria) greatly accelerate chemical weathering and mediate the formation of secondary minerals, but their relative *in situ* contribution is difficult to identify (Taylor et al., 2009). According to Pawlik et al. (2016), biochemical weathering prevails on mechanical weathering for two reasons. First, the main microorganisms implied in this process are widespread, can survive under extreme conditions, and can colonize niches unattainable by other organisms. Second, the fungal hyphal network associated with roots highly increases the space potentially subjected to biochemical weathering. Soil organisms act both directly and/or indirectly on weathering, either by producing compounds (organic acids, phenolic compounds, and protons) and/or by stimulating the activities of microorganisms that further accelerate weathering. Five key mechanisms of weathering exist: (1) root exudates containing protons and organic acids, (2) CO_2 release from root respiration, (3) organic acids and chelators from organic matter decomposition, (4) evapotranspiration that increases the flow of water bearing base cations and other nutrients to plants, and (5) reduction of erosion that also allows further soil development (see section 4.2.2).

Focusing on exudates, Landeweert et al. (2001) reported that low molecular weight organic acids produced by plant roots, bacteria, and fungi are considered to be the most important biological weathering agents in soils, driven by their acidifying and complexing capacities. Due to their high acid strength, citrate, malate, and oxalate are the strongest chelators of metals, including Al^{3+}, a central element in most mineral crystal lattices. All these organic acids are largely produced by fungi, bacteria, and roots, especially proteoid roots (Weisskopf et al., 2008). By contrast, medium- to high-molecular-weight organic acids, such as humic substances, are less effective for the dissolution of minerals.

Schulz et al. (2013) underlined that most of the studies on the role of microorganisms in weathering were obtained through laboratory experiments and do not allow predicting the rates of weathering under field conditions. The rare field researches were conducted in pioneer stages of soil formation, as for example in the forefields of retreating glaciers, where biofilms of bacteria dissolve the siliceous bedrock by exuding organic acids (Schulz et al., 2013). Lichens also enhance the transformation of feldspars to clay, and mosses generally produce a great abundance of expandable clay minerals. Finally, Pawlik et al. (2016) suggested that mycorrhizal and saprotrophic fungi participate in weathering of feldspars and hornblends in granitic bedrocks and E horizons of podzolic soils.

4.2.1.2. Earthworms

4.2.1.2.1. Mineral weathering. The mean grain size of minerals in aggregates produced by earthworms is generally smaller than in the surrounding soil. This difference results from (1) a mechanical breakdown of mineral grains during their passage through the earthworm gut, or (2) a selective ingestion by earthworms (Curry & Schmidt, 2007; Edwards & Bohlen, 1996; see section 4.1.2). Actually, several experimental studies have shown the ability of earthworms to mediate mineral weathering. Suzuki et al. (2003) showed that pellets produced by epigeic earthworms (*Eisena fetida*) contain smaller and rounder grains than noningested grains. Moreover, due to its hardness, the disintegration of quartz is slower than that of K-feldspath. The mechanism of mineral weathering is, however, still unclear. It is unlikely due to proton dissolution because the earthworm's gut is at near neutral pH, probably promoted by a ligand produced by a digestive enzyme of the earthworm or by microbes contained in the earthworm's gut (Carpenter et al., 2007). However, earthworm species may play a role as demonstrated by Hodson et al. (2014). In this study, the anecic *Lumbricus terrestris* seems not to affect mineralogy, whereas both the epigeic *Eisenia veneta* and the endogeic *Allobophora chlorotica* clearly accelerate mineral weathering, especially on primary silicates (anorthite, biotite, and olivine) compared to secondary minerals (kaolinite, illite, and smectite).

4.2.1.2.2. Calcium cycling. Several authors underlined the role of earthworms in the biogeochemical cycling of calcium in soil. Many species secrete granules of calcium carbonate ranging from single calcite crystals to agglomerated granules up to 2.5 mm in diameter (Canti & Piearce, 2003). The rate of granule production differs between species and varies according to physico-chemical properties of the surrounding soil. Under suitable conditions, such granules are often preserved from dissolution, remain in soils for decades to thousands of years, and constitute a small but significant component of calcium storage in soil (Lambkin et al., 2011).

4.2.2. Soil Structure Formation, Stabilization, and Disintegration

Soil structure relates to the spatial arrangement of mineral and organic particles and their associated pores into groupings called aggregates or peds (Oades, 1993). Churchman (2010) considers that aggregation is a specific feature of soils and plays a fundamental role in terms of soil functioning. In fact, a well-developed structure can improve biodiversity in ecosystems; positively affect water storage capacity, infiltration, and aeration in soil; promote plant uptake and root growth; and increase the resistance to soil erosion.

There is a long history of research about aggregation processes (Six et al., 2004). In 1982, Tisdall and Oades proposed the concept of aggregate hierarchy that distinguishes primary particles (< 20 microns), microaggregates (20–250 microns) and macroaggregates (> 250 microns). This hierarchical concept is used worldwide (Totsche et al., 2018; Lehmann, Leifheit, et al., 2017; Lehmann, Zheng, et al., 2017), but soil aggregation is still a complex process that is controlled by an interplay of physical processes affecting the ecosystem, soil physicochemical parameters (texture, amount of organic matter, calcium carbonate content, etc.), soil organisms, and interrelated factors: physical (drying-wetting, freezing-thawing), chemical (binding agents), and biological (fauna, roots, and microorganisms).

4.2.2.1. Soil structure and biota The chemical, physical, and biological effects of different key organisms (earthworms, termites, fungi, plant roots) in the formation, stabilization, and disintegration of soil structure has been recognized for decades. Biochemical mechanisms include particle adhering and orientation, surface sealing, and particle surface hydrophobicity. Biophysical mechanisms refer to soil compaction and compression, particle grinding and remolding, changes in water content, and particle entanglement by fungal hyphae.

4.2.2.2. Plants and soil aggregation Aggregation processes can be divided into five mechanisms that can interact and are dependent on the size of aggregates, namely, (1) root penetration, (2) changes in soil water regime, (3) agglutination, (4) dead root decomposition, and (5) root entanglement (Six et al., 2004). Several reviews discuss root-related processes that affect soil structure formation, stabilization, and disintegration (Angers & Caron, 1998; Degens, 1997; Six et al., 2004).

4.2.2.2.1. Root penetration. Root growth in pores and the soil matrix generates compressive and shear stresses, which can reach up to 2 MPa (Angers & Caron, 1998). Radial compression may reorient clay particles in the close

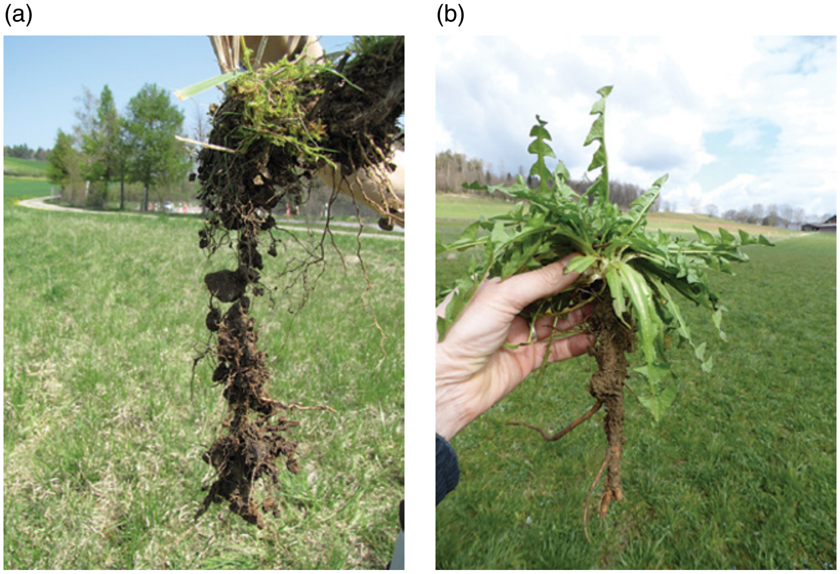

Figure 4.2 Two different root systems. (a) Well-branched roots of *Lolium sp*. (b) Taproot system of *Taraxacum sp*. Photos: Claire Le Bayon.

vicinity of roots, mostly in a 50–200 μm zone. These clay particles are then bound together by extracellular polysaccharides secreted by roots that induce the formation of microaggregates. By contrast, root penetration into relatively unstable macroaggregates may divide them in small units, thus decreasing the proportion of large aggregates. Depending on the type of vegetation, and especially root architecture (Figure 4.2), the overall influence of root penetration on aggregation may vary (Six et al., 2004). Similarly, the growth of fungal hyphae exerts a pressure on the surrounding soil and can potentially push and move particles and aggregates. However, there is still no report on this mechanism in either mycorrhizal or nonmycorrhizal fungi (Lehmann, Leifheit, et al., 2017).

4.2.2.2.2. Changes in soil water regime. Variations in frequency and amplitude of dry-wet cycles generally promote the formation of aggregates in soils. Six et al. (2004) cited a decrease (in the order of 10% to 20%) in aggregation due to changes in soil water status, for instance: (1) the water absorption by plants induces localized drying effects, which can promote bonds between root exudates and clays; (2) root exudates reduce the wetting rate by occluding pores or increasing pore tortuosity; (3) a preferential water flow occurs along living roots. Consequently, the shape of aggregates may differ; hence, physicogenic macroaggregates formed under sterilized, moist (20% of water holding capacity) conditions appear planar and angular at both macro- and microscales (Blankinship et al., 2016). In contrast, biogenic macroaggregates formed under live, dry (10% of water holding capacity) conditions are spherical with rounded edges. Lehmann, Leifheit, et al. (2017) hypothesized that mycorrhizal fungi may also affect the aggregation process by changing the soil water status. Water fluxes between the host plant and its symbionts can alternatively result in dampening or drying the soil of mycorrhizosphere.

4.2.2.2.3. Agglutination of particles and aggregates. Many products act as agents capable of gluing, or agglutinating, particles or aggregates. Transient (e.g. organic materials), temporary (e.g. roots, hyphae, and bacteria), and persistent compounds (e.g. amorphous iron and aluminum, aromatic humic material, complexes of clay-polyvalent metal-organic matter) perform as binding agents for aggregates (Tisdall & Oades, 1982). Anyway, their composition and origin have not yet been fully established.

According to Totsche et al. (2018), "gluing agents include all organic substances (e.g. polysaccharides, proteins, extracellular polymeric substances) responsible for the agglutination of subunits forming a micro-aggregate or a composite building unit". Fungi and bacteria secrete mucilaginous products containing polysaccharides and root exudates, which stimulate microbial activity and tight interactions between roots and microbes in the rhizosphere.

4.2.2.2.4. Dead roots. The decomposition of dead roots also promotes both aggregation and macropores, which can significantly influence moisture dynamics. Six et al. (2004) reported that most of the stable aggregates are formed after the senescence phase and not during the vegetative one. The magnitude of this effect depends on both the amount and decomposability of organic material.

4.2.2.2.5. Entanglement by root and fungal hyphae. Lehmann, Leifheit, et al. (2017) underlined that despite the evidence of this mechanism for both formation and stabilization of macroaggregates, entanglement by roots and fungi is still very poorly documented. One of the reasons is the difficulty of disentangling the influence of entanglement from other associated processes, in particular exudation promoted by roots and fungi. The mycelial meshwork helps to stabilize enmeshed soil and aggregates, and hyphae confer shear resistance and tensile strength to soil units. In addition, the regenerative capacity and longevity of mycelia increase their resistance against disturbances. With time, soil structure changes and unstable macroaggregates can thus disintegrate into microaggregates due to the penetration of roots. In addition, vesicular arbuscular mycorrhizae (VAM) could also participate to degrade mucilages and thus destabilize aggregates. However, data measuring the turnover of aggregates are still rare.

4.2.2.3. Implication of plants in organic matter stabilization

According to traditional viewpoints, organic matter persists in soil for a longer or shorter time depending on its chemical complexity and composition. New models about the persistence of organic matter in soil have recently emerged (Schmidt et al., 2011). Indeed, molecular structure alone does not control C residence times, as C stability mainly depends on the physicochemical and biological environment (water availability, pH, presence of degraders, etc.). The key role of roots and rhizosphere in the dynamics of organic matter is also emphasized. First, plant roots and rhizosphere inputs make a large contribution to soil organic matter. Second, root-derived C would be more retained than aboveground inputs (leaves or needles). Third, root and mycorrhizae are very efficient in physicochemical interactions with soil particles. Finally, the fresh root inputs could be considered as primers leading to a more rapid decomposition of older organic matter.

4.2.2.4. Earthworms and soil aggregation

By moving in the soil matrix and mixing, ingesting, and excreting soil and organic matter particles, earthworms create biogenic structures, such as burrows and casts (Lavelle et al., 1997). Through their selective feeding behavior, earthworms ingest fine organic and/or mineral particles and contribute to organic matter degradation and intimate incorporation to clay and silt (Brown et al., 2000). Casts and burrows thus form new habitats usually enriched in organic matter and nutrients that act as hotspots of biological activity. Endogeic and anecic earthworms are particularly implied in aggregate and burrow buildup, whereas epigeic species localized in hol-organic layers create mainly organic pellets (Bouché, 1977; Lee, 1985). Earthworm activity depends on both soil temperature (Uvarov et al., 2011; Whalen et al., 2004) and moisture (Edwards & Bohlen, 1996; Kanianska et al., 2016), and they tend to decrease their activity substantially in summer (Potvin & Lilleskov, 2017). However, species such as *Lumbricus terrestris* may remain active throughout winter.

4.2.2.4.1. Mucus and gut processes. At the body surface and in the forepart of the gut, earthworms secrete polysaccharide compounds called mucus (Chapuis-Lardy et al., 2011; Lee, 1985). The amount or quality of the epidermal mucus may vary according to ecological earthworm categories and ingested substrates (Trigo et al., 1999). The mucus of *Allolobophora chaetophora* is, for instance, composed of 69% proteins and peptides and 31% carbohydrates (Cortez & Bouché, 1987). Zhang et al. (2016) demonstrated that mucus samples from three earthworm species (*Eisenia fetida*, *Aporrectodea trapezoides*, and *Amynthas pingi*) may contain 16 amino acids that could activate microorganisms (Bityutskii et al., 2012; Blouin, Hodson, et al., 2013; Chapuis-Lardy et al., 2011; Shipitalo & Le Bayon, 2004). The exoenzymes produced by ingested microorganisms enhance the degradation of complex organic matter during its passage through the gut and thus enhance the capacity of the worm to assimilate nutrients (Edwards, 2004). Moreover, *Lumbricus terrestris* has its own enzyme pool, independent from the microorganisms present in the ingested soil; this is notably the case for alcaline phosphatases implied in organic phosphorus mineralization (Le Bayon & Binet, 2006).

4.2.2.4.2. Cast production. According to Lee (1985), earthworms can process up to 25% of the A horizon in 1 year through the production of casts within the soil profile and onto the surface (often called surface casts or middens when particularly enriched in organic matter debris; see Figure 4.3). Most of the studies focused on surface casts whose amount of production may reach a mean of 40,000 kg/ha/yr (based on 19 studies; Feller et al., 2003). In a maize plot, Le Bayon and Binet (1999) calculated that surface-cast production may reach 34 kg dwt/yr per kg of earthworms (fwt) in the presence of anecic *Lumbricus terrestris* and the endogeic *Aporrectodea caliginosa* as the dominant species. In a grassland in Luxembourg, a total amount of 195.6 ton/ha of casts was measured, 58% from endogeic earthworms and 42% from anecics (Zangerlé et al., 2016). According to Zorn et al. (2008), endogeic species may deposit up to 95% casts underground. Therefore, earthworms act as a living bioreactor, and the duration of digestion probably affects the first step of microaggregate disruption before being remoulded in larger aggregates (Six et al., 2002, 2004). As example, the pressure applied to soil may reach 259 Pa in

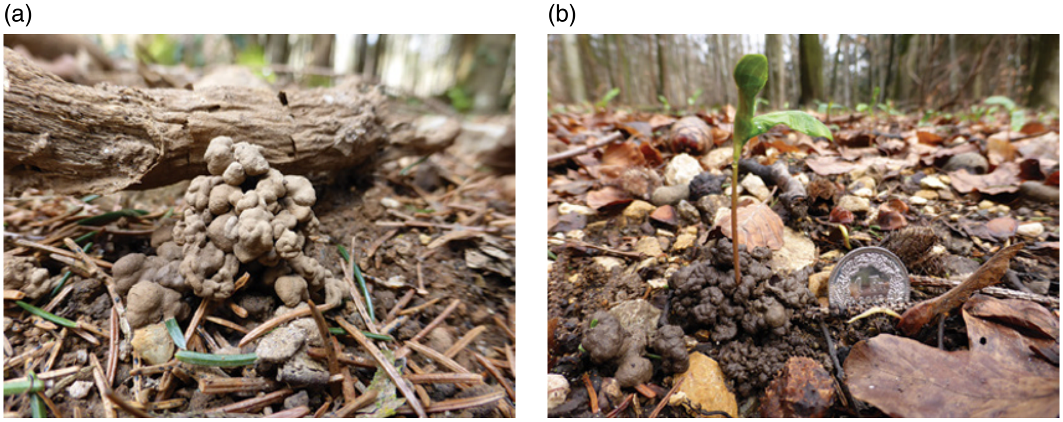

Figure 4.3 Surface-casts of anecic earthworms. (a) Different colors of structures indicate the variable organic matter content. (b) Casts constitute hotspots of available nutrients for plant growth, here beneficial for a seedling of *Fagus sylvatica*. Photos: Claire Le Bayon.

the gut of *Aporrectodea rosea* (McKenzie & Dexter, 1987) and, concomitant to the addition of mucus, can lead to the disruption of existing interparticle water and cation bridges within aggregates (Shipitalo & Protz, 1988, 1989). Consequently, the soil fabric is reorganized in the intestines of earthworms (Barois et al., 1993), and this remolding, combined with the high water content, may explain why fresh, moist casts are usually less water-stable than non-ingested soil (Le Bayon & Binet, 2001; Le Bayon et al., 2002; Marinissen & Dexter, 1990; Shipitalo & Protz, 1988). With time, casts are stabilized by a combination of physical (thixotropic hardening), chemical (secretion of amorphous calcium carbonate as a binding agent), and biological processes (microbial polysaccharides). This stabilization also depends on earthworm species, and Schrader and Zhang (1997) noted that water-stable aggregation is significantly higher in casts of *Lumbricus terrestris* than in casts of *Aporrectodea caliginosa*. They also noticed that the tensile strength of casts is positively correlated with the clay and carbonate content of the parent soil, while for water-stable aggregation the correlation is inverse. The initial soil texture also plays a major role in cast content (see section 4.1.2). In pioneer environments such as floodplains with regular sediment deposits, epigeic earthworms (mainly *Lumbricus rubellus*) are the first engineers involved in soil structure in the short term. If the texture is favorable (mostly silt dominated), anecic and endogeic earthworms may then colonize the different soil layers, improving physical and nutrient conditions and creating long-term stable aggregates (Bullinger-Weber et al., 2007).

4.2.2.4.3. Burrowing. Burrows (Figure 4.4) result from two main processes: (1) the soil is crumbly enough to allow earthworms to dig into it without ingesting it or (2) the soil is so compact that they have to ingest it before excreting casts. Through peristaltic movements (Lee, 1985), earthworms exert a strong lateral pressure to push particles aside during burrow construction, and anecic species such as *Lumbricus terrestris* and *Aporrectodea nocturna* but also the endogeic *Aporrectodea caliginosa* are especially efficient in this process (Edwards & Bohlen, 1996). The speed of burrowing depends on soil texture, a silty texture being more favorable than a clayish one (Edwards, 2004), but also on temperature, water content, and topography, as well as on ecological categories (Bastardie et al., 2005; Perreault & Whalen, 2006). Capowiez et al. (2015) showed that endogeic earthworms make more extended burrow systems, which are more highly branched, less continuous, and of smaller diameter than those of anecic earthworms. Three main characteristics significantly influence water infiltration: burrow length, burrow number, and bioturbation volume, but the connectivity of galleries seems also essential to ensure efficient hydraulic conductivity (Pérès et al., 2010).

Estimations of the number of burrows in temperate regions range from 100 to 800 per square meter (Lavelle, 1988), with a mean ranging between 50 to 200 burrows per square meter (Edwards & Bohlen, 1996). Some species such as *Lumbricus terrestris* make nearly vertical permanent burrows up to 12 mm in diameter and 2.4 m deep in which they can live over several years (Edwards & Bohlen, 1996; Lavelle & Spain, 2001; Lee, 1985). *Lumbricus terrestris* intensively reuses its continuous, vertical burrows (Grigoropoulou & Butt, 2012; Nuutinen, 2011). These burrows can have several entrances, as they are directly underneath surface casts, which can block the entrance. Earthworm burrows function as soil macropores, improving soil aeration (Knight et al., 1992), infiltration (Stockdill, 1966), and water-holding capacity, especially in casts and burrow linings. Quantifying the number of burrows or soil macropores might thus be a

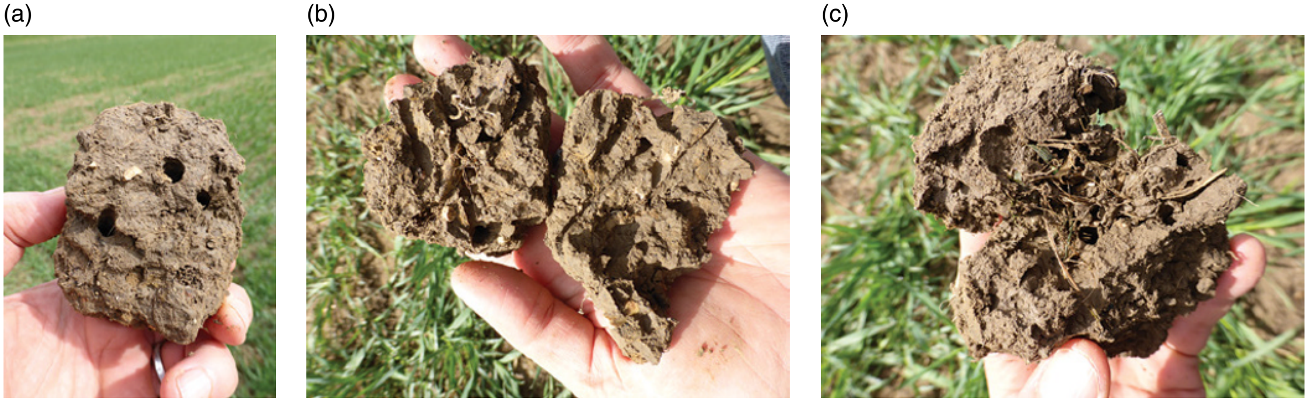

Figure 4.4 Burrows of anecic earthworms. (a) Burrow openings of anecic earthworms. (b) Burrow linings when the soil clod is cut in two parts. (c) Coarse fragments of organic matter are clearly visible inside worm galleries. Photos: Claire Le Bayon.

good indicator of current or past earthworm activity (Pérès et al., 2010).

4.2.2.4.4. Aggregate disintegration. When polysaccharides and other organic gluing agents are mineralized, the breakdown of soil macroaggregates increases over time (Ge et al., 2001; Guggenberger et al., 1996). Surface casts are primarily disrupted by climatic events, such as raindrop impacts and wet-dry cycles (Binet & Le Bayon, 1998; Le Bayon et al., 2002), by cattle trampling (Decaëns, 2000), when small earthworms such as Eudrilidae and enchytraeids dig burrows into the casts (Blanchart et al., 1997; Topoliantz et al., 2000), or if casts themselves come unstable as soon as they are produced. The case of belowground casts of *Metaphire posthuma* was highlighted by Botinelli et al. (2010). As they disintegrate, these weak casts are more susceptible to dispersion and may lead to a rapid compaction of the soil after rainfall events, especially in Asia due to the high intensity of monsoon rainfall. This subsequent formation of a compact and impermeable layer was well studied in tropical regions by Blanchart et al. (1997, 1999) and Chauvel et al. (1999). Blanchart et al. (1997) and Rossi (2003) also showed the existence of "compacting" earthworm species versus "decompacting" species that play a key role in the regulation of savannah soil structure. Compacting species produce large globular casts that are expected to compact the soil, whereas decompacting species produce fine granular casts that can decrease soil bulk density (Blanchart et al., 1993, 1997). Guéi et al. (2012) demonstrated that despite the presence of both, soil water infiltration rate may increase. Thus, the preservation of earthworm species belonging to contrasting functional groups appears essential for the maintenance of stable soil structure in agro-tropical ecosystems (Guéi et al., 2012).

4.2.3. Bioturbation due to Plant and Earthworm Activities: Impacts on Soil Differentiation and Development

The concept of bioturbation in soil was initially introduced by Darwin (1881) for earthworms and Schaler (1891, in Wilkinson et al., 2009) for plants. Bioturbation by terrestrial organisms generates the physical displacement of materials and results in a redistribution and reorganization of these components, as well as a dissemination of organisms in soil. Wilkinson et al. (2009) classified bioturbation into primary processes (soil production, soil mixing) and secondary processes (mounding) resulting from previous ones. Soil production occurs both directly by mass displacement and indirectly by weathering of parental material. Soil mixing refers to material movements within or between soil horizons, and mounding to depositions on the soil surface (Wilkinson et al., 2009). Moreover, abiotic processes (aeolian and water erosion) and biotic ones (dismantlement of mounds by predators or by cattle trampling) affect redistribution of soil in mounds. In addition, secondary fabric features (burrows, root channels) result from recent and/or past bioturbation within or between horizons (Wilkinson et al., 2009).

Present at different spatio-temporal scales, bioturbation can contribute to a progressive or a regressive pathway of soil development (Gobat & Le Bayon, 2013), but until now only few models integrate the calculation of soil development rates. Alexandrovskiy (2007) applied such a turbational model to Chernozems, soils in which horizon mixing by burrowing animals is particularly remarkable.

For each ecosystem engineer (first plants and then earthworms), we describe in the following sections (1) the mechanisms of bioturbation taken in consideration, (2) the effects of bioturbation on soil heterogeneity at different spatial scales, and (3) the effects of bioturbation on soil development. Finally, a discussion about their effects on pedogenesis pathways (trajectories) is tackled.

4.2.3.1. Bioturbation by plants: Mechanisms

Gabet et al. (2003) identified five mechanisms of bioturbation performed by plants: (1) root expansion during growth, (2) decay and infilling of former root channels, (3) settling of the soil due to water extraction by roots, (4) agitation of the plant during storms, and (5) uprooting. The first three mechanisms occur within a horizon at different spatial scales, ranging from mineral particles to aggregates (see sections 4.2.1 and 4.2.2). While agitation is poorly known, uprooting is better understood. This mechanical process is due to wind, snow overload, root decomposition, or fall of adjacent trees. The probability that trees are uprooted is a function of soil depth, and is maximum for shallow soils (about 35 cm depth), and then decreases to nil for soils over 1.5 m depth (Gabet et al., 2003). This phenomenon has been especially studied in Podzols, whereas little research was conducted on Cambisols or on soils with hydromorphic features (Kooch et al., 2015; Kooch, Hosseini, et al., 2014; Kooch, Zaccone, et al., 2014; Šamonil et al., 2015; Šamonil, Král, et al., 2010; Šamonil, Tejnecký, et al., 2010; 2015; Schaetzl et al., 1990). The uprooting and fall of a tree usually creates a pit where the roots were previously located and an adjacent mound resulting from slumping of the displaced and decaying root plate (Figure 4.5). Slump and erosion of material from the root plate are known as bioturbation processes. The paired pit/mound system is highly variable in size and longevity and the study of its chronosequences provides a good understanding of the effects of uprooting over time (Bormann et al., 1995; Coyle et al., 2017; Kooch et al., 2015; Kooch, Hosseini, et al., 2014; Kooch, Zaccone, et al., 2014; Pawlik et al., 2016; Šamonil et al., 2015; Samonil, Král, et al., 2010; Šamonil, Tejnecký, et al., 2010; Schaetzl et al., 1990; Valtera & Schaetzl, 2017). Moreover, cross-sectional drawings of pit/mound pairs describe changes in spatial patterns. Depending on climatic conditions and site characteristics, this system covers from 0.1% to 90% of the forest area and its total disintegration can be very rapid (5 to 10 years in humid tropics) or can exceed 500 to 1000 years in many other environments. Consequently, the effects of uprooting on soil heterogeneity and soil development are thus highly variable (Schaetzl et al., 1990).

Figure 4.5 Tree uprooted following a wind event two years ago. Soil (Cambisol) and calcareous stones are still attached to the roots (east of France). Photo: Claire Guenat.

4.2.3.2. Bioturbation by plants: Effects on soil heterogeneity and soil development

According to Pierret et al. (2007), root growth reorients and packs particles, and enhances macroporosity. By (re) using paths of less mechanical resistance, including former root channels, root growth leads to the formation of a specific environment, which significantly differs both chemically and biologically from the bulk soil. Water uptake by plants can also induce moisture gradients that, depending on soil texture and mineralogy, contribute to increase soil heterogeneity. These *in situ* mechanisms generate transformations leading to displacement of materials over a very short distance (Blum et al., 2018). At the pedon scale, tree uprooting can change the spatial arrangement of soil, from single horizons to the entire soil profile, which can be completely reversed or even destroyed. Moreover, the heterogeneity of the soil profile is increased by the displacement of stones, brought to the soil surface and then buried under deposits produced by collapse of the root plate and erosion (Schaetzl et al., 1990). Uprooting may also modify chemical and biological properties, especially in pits and mounds that differ compared to adjacent and undisturbed soils. For example, in a beech forest in northern Iran, Kooch, Hosseini, et al. (2014) showed that organic C, total N, water content, microbial respiration, texture, density, and biomass of earthworms are significantly greater in pits than in mounds and undisturbed soils.

4.2.3.3. Postuprooting pedogenesis

The effects of uprooting diminish over time and new sequences of horizons, reflecting the process of postuprooting pedogenesis, are gradually developed. According to Šamonil et al. (2015), progressive soil development is generally observed, whereas regressive development is rare, but pedogenetic processes in pits and mounds can show diverse evolutionary trajectories. The evolution is nonlinear, and postuprooting pedogenesis is more rapid in pits because weathering is generally more efficient (Šamonil et al., 2015; Schaetzl et al., 1990). In podzolic soils, postuprooting pedogenesis is determined by C dynamics (accumulation versus decomposition) driven by the frequency of disturbance (Bormann et al., 1995). Similar divergences of pedogenetic trajectories are also reported by Schaetzl et al. (1990) for other types of soils (Inceptisols instead of Podzosols) and extrapolations, as well as simulations of soil development, thus remain challenging (Šamonil et al., 2015).

4.2.3.4. Bioturbation by earthworms: Mechanisms and rates

All processes of bioturbation are carried out by earthworms relative to ecological activity, species, and also abundance and biomass. The first assessments come from Darwin (1881) in the United Kingdom, with annual rates (ton/ha) of 19–40 for mounding, 26 for mixing, and 2–152 for burial of soil. Also in the United Kingdom, Evans (1948) estimated mounding rates from 3 to 63 tons/ha/yr and mixing rates from 5 to 53 tons/ha/yr. In France, Bouché (1981) obtained equivalent rates (20 tons/ha/yr) for mounding and mixing. Finally, in Australia, under humid subtropical conditions, mixing rates reach 127 tons/ha/yr, while mound rates are very low (5–6 tons/ha/yr).

4.2.3.5. Bioturbation by earthworms and pedogenesis

According to Cunha et al. (2016), earthworms affect pedogenesis in two main ways: first by modifying soil profile through bioturbation and second by their effects on decomposition and nutrient cycling. Earthworms need from 5 to 20 years to turn over once the topsoil (0–30 cm) in grasslands under temperate climate. For the same climate conditions, Feller et al. (2003) suggested that earthworms can potentially move about 40 cm of soil to the surface each century. As burrows facilitate the transfer of water, air, and nutrients, earthworm bioturbation enhances organic matter incorporation and microorganisms' redistribution, which in turn enhances the homogenization of the soil's profile and properties. However, material movements by earthworms is greater in the uppermost layers than in deeper soil layers (Muller-Lemans & van Dorp, 1996). Consequently, both structuration and accumulation of organic matter occur mainly in topsoil. Besides, the composition of casts differs from the surrounding soil, increasing thus soil heterogeneity (Pierret et al., 2007). Finally, as coarse materials (gravels, stones) cannot be ingested by earthworms, they tend to be gradually buried under topsoil casts and may thus form a stone layer, increasing soil profile differentiation (Wilkinson et al., 2009).

4.3. PLANTS AND EARTHWORMS CONTRIBUTE TO SOIL ECOSYSTEM SERVICES

The notion of ecosystem service (ES) is increasingly used in the evaluation of environmental sustainability. ESs are commonly defined as the "benefits people obtain from the ecosphere and its ecosystems" (MEA, 2005) and are listed in four broad categories: provisioning (e.g. production of food and water), regulating (control of water, climate and disease, C sequestration), cultural (spiritual and recreational benefits), and supporting services (e.g. habitat, biodiversity, nutrient cycles). The first three categories directly affect people, whereas the supporting services are there to maintain the other services (Dominati et al., 2010).

4.3.1. Provisioning Services

There is a strong link between soil and agricultural productivity, and therefore most studies about soil-related ESs include an assessment of provisioning ES such as biomass production (da Silva et al., 2018). Many components of biodiversity affect ES delivery. For example, earthworms act as catalysts in improving crop yield, but their performance depends on the amount of crop residues, earthworm density, and rate of fertilization (Sharma et al., 2017). On their side, plants influence soil by the vast majority of organic matter upon which the rest of soil life depends, and they also deform the soil under the mechanical action of roots by elongation or radial growth (Briat & Job, 2017).

In a meta-analysis about the effect of earthworms on plant production across the globe, van Groenigen et al. (2014) showed that earthworms favor the availability of N from crop residues that stimulate plant growth. In this case, organic fertilizers prevail over inorganic ones. In another study reporting an inoculation of *Lumbricus terrestris*, the effect on plant productivity was increased by 20% to 60% of both plant cover and biomass (Forey et al., 2018). van Groenigen et al. (2014) also mentioned that in pastures with presence of plants capable of symbiotic N_2 fixation such as legumes, the positive effect of earthworms was smaller, and their influence on pasture productivity disappeared. Earthworms are also known to increase phosphorus availability in their casts and burrows (Le Bayon & Milleret, 2009). Earthworm density also has a significant effect on aboveground plant biomass, particularly at high densities (> 400 individuals per m^2; van Groenigen et al., 2014). In pots containing homogenized and repacked soil, the earthworm effect on aboveground biomass was almost twice as high as in undisturbed soils, meaning a positive effect on plant growth and thus on productivity (van Groenigen et al., 2014). Management practices with objectives of sustainable intensification of agriculture should be encouraged to maintain earthworm populations in good health. For example, low-input farming systems in the tropics, and to a lesser extent organic farming systems, vary in terms of habitat quality for earthworms (van Groenigen et al., 2014), and large application rates of organic manure of high-quality crop residues provide excellent conditions for bioturbation. Tillage can also have detrimental effects on soil life, especially when the soil is inverted, leading to strong effects on soil organisms such as epigeic earthworms (Orgiazzi et al., 2016). No-till systems may thus support larger and more diverse earthworm communities. Epigeic and anecic species particularly benefit from no-till, as endogeic ones may support tillage systems that incorporate crop residues. Earthworms are also affected by tillage frequency: physical injuries or death by tools, exposure to predators and/or desiccation or frost by soil inversion, destruction of burrows, changes in soil physical conditions, and soil compaction (Orgiazzi et al., 2016).

Plants also contribute meaningfully to provisioning ESs because they are the major source of C inputs into the soil through litterfall and whole-plant senescence, as well as root-derived C loss by living plants (Bowsher et al., 2018). In fact, root exudates and sloughed-off cells influence N availability (mainly nitrates) and thus plant growth (Jackson et al., 2008). Therefore, when N supply and access is high through nitrification, N losses may be lower, thereby increasing the provisioning services provided by plant-microbes-soil transformations without any application of fertilizers (Jackson et al., 2008). Moreover, plant roots in up to 80% of plant families may establish symbiotic interactions with VAM that not only improve the growth of plants through uptake of available soil phosphorus and other mineral nutrients but also prevent erosion by stabilizing aggregates (Gianinazzi et al., 2010). However, management practices as soil tillage negatively affects VAM through different mechanisms such as propagation, extraradical hyphae, and colonized root segments. Tillage also destroys the mycelial network and affects nutrient acquisition, especially during early stages of crop growth (Orgiazzi et al., 2016). In this context, future prospects on sustainable management have to be considered. In fact, by 2050, the global population is projected to be 50% larger than now with a global grain demand that follows this trend. Further increases in agricultural yields are essential but not at the cost of losing important ecosystem functions. Due to their great diversity, soil organisms such as earthworms and plants offer many resources, but this natural capital must be further investigated in order to preserve them and evaluate the range of possible strategies.

4.3.2. Regulating Services

4.3.2.1. Health and soil fertility

According to FAO (2015), "healthy soils are a basic prerequisite to meeting varied needs for food, biomass (energy), fiber, fodder, and other products and to ensuring the provision of essential ecosystem services in all regions of the world." In this context, biodiversity is among the main factors responsible for the provision of regulating and supporting ESs. Earthworms and plants are important in maintaining soil health, and higher plants are the major primary producers of biomass, C, and energy released into the soil. According to FAO (2015), earthworms could give general indications of relative changes in soils and may thus be considered as indicators and should be included in the global soil health monitoring scheme. Moreover, they have been shown to enhance soil fertility through a variety of mechanisms including increased nutrient availability, enhanced soil aggregation, and water availability, as well as improved stress tolerance and pest regulation (Fonte et al., 2019). Earthworms also degrade and decompose dead organic matter through mineralization that takes place in their guts, thus enhancing natural stocks of nutrients available for soil biota for chemical reactions, which enables humans to live in a stable, healthy, and resilient environment (Dominati et al., 2010).

4.3.2.2. Water infiltration

Plant roots and earthworms greatly influence soil formation and maintenance by the creation of soil structure (see section 4.2), particularly at the very first stages of pedogenesis, providing physical support to plants, animals, and human infrastructures. Pioneer plants allow accumulation of organic matter from their dead materials essential for the development of a first soil horizon, the A layer, and contribute to soil stabilization through the physical action of very fine roots. Earthworm burrows in the upper layer are suitable for root growth. With their foraging activity, earthworms create preferential flow paths for water, thus decreasing propensity for overland flow, which leads to a reduction of erosion risk, especially in mature soils where large amounts of water infiltrate and are retained in the pore spaces.

However, due to continuous alteration and erosion processes, new soils are formed while old ones are slowly disaggregated by erosion. The notion of inherited and newly formed soils can be illustrated through floodplains submitted to perturbations such as flood events. Plants in particular are very efficient at agglutinating organic and mineral particles and thus increasing topsoil structural stability (Schomburg, Schilling, et al., 2018; Schomburg, Verrecchia, et al., 2018). This is of crucial importance in the case of floodplain restoration projects that aim to rehabilitate water flow regulation, meaning attenuation of runoff and discharge rates, water storage for flow regulation, and mass flow regulation (i.e. erosion protection). For example, Schindler et al. (2016) indicated that renaturation has strong positive impacts on other regulation services such as lateral floodplain reconnection and creation of natural habitats, which is of particular importance in biodiversity conservation.

In fact, earthworms and plants have a great influence on flood mitigation. Soil structure and more precisely macroporosity play a major role in soil water infiltration and processes related to the control of drainage runoff (Pelíšek, 2018). Earthworms also interact with plant species composition, and certain plant functional groups could significantly alter variations in soil hydraulic properties. According to Fischer et al. (2014), soil infiltration capacity increases with legumes but decreases with grasses, probably due to roots that modify the pore structure. Further, legumes enhance earthworm activity while grasses suppress it. Functional groups of plants may thus affect earthworm and root activities.

The role of plants in soil hydraulic properties is also important for water extraction from deeper layers through roots. Plants adapt to drought by rapidly developing fine roots or by increasing the activity and efficiency of deep roots, which are responsible for water uptake (Teuling et al., 2006). Transpiration is also a key to understand ecosystem functioning and particularly the efficiency of plants to use and store water. Models are usually prevalent (Guderle & Hildebrandt, 2015) with assumptions to determine the sink term for root water uptake in soil water flow models. In this way, standard measurements (e.g. soil water content profiles) are used for the estimation of evapotranspiration and root water uptake. Through transpiration, plants act as a natural regulator of water fluxes between soil and atmosphere, and these fluxes allow as much as 60% of whole land precipitation to return to the atmosphere (Javaux et al., 2013).

4.3.2.3. Tritrophic interactions

Soils provide habitat for thousands of species that regulate pest control and dangerous disease vectors (Dominati et al., 2010). This regulating ES is principally related to soil properties and the biological processes driving inter- and intraspecific interactions (symbiosis, competition). As an example, Blouin et al. (2005) emphasized the importance of belowground interactions in plant ecophysiology. In a controlled experiment, the decrease in rice growth caused by a parasitic nematode was suppressed in the presence of earthworms. Earthworms thus enhanced the tolerance of roots to nematodes, and the expected inhibition of photosynthesis was suppressed. It has also been shown that earthworms are also able to generate hormones and subsequently may render a plant tolerant to parasitic nematodes by inhibiting the gene responsible for the repair of damaged roots, preventing plant death after all leaves have shrivelled (Orgiazzi et al., 2016). More generally, the preservation of existing natural enemies by choosing cultural, mechanical, or selective chemical controls that do not harm beneficial species should be favored (Orgiazzi et al., 2016). With their capacity for creating plant-microbe interactions, plants also present benefits in terms of disease reduction. They may specifically attract microbes for their own benefit as, for example, through the recruitment of different groups of plant-associated microbes that promote plant growth. These microbes then undergo host-specific adaptations, such as highly specialized mutualism leading to a better tolerance to pathogens (Orgiazzi et al., 2016).

4.3.2.4. Pollution control

Soil invertebrates can also be used as indicators of land use, soil fertility, or soil pollution. Their size, limited rapidity in soil displacement, and slow recolonization make them attractive as bioindicators (Paoletti, 1999). Indeed, earthworms are currently considered good environmental indicators or biomarkers of pollution exposure (Pérès et al., 2011).

Earthworms have been applied to the bioremediation of heavy metal pollution. Indeed, some earthworm species are tolerant to heavy metals and can perform their ecological functions and complete their life history in contaminated soil (Mo et al., 2012; Xu et al., 2018). For instance, *Amynthas gracilis* allowed evaluating the bioavailability and ecotoxicity of many soil pollutants (Parelho et al., 2018). Actually, earthworms provide a realistic indication of pollution as they are exposed to soil pollutants in both the soil surface and the deeper topsoil layers through their epi-endogeic activity. This permits an integrated overview of the biological effects of livestock soil pollutants on soil organisms.

When plants perform bioremediation, this cleaning service is called phytoremediation. First, some plants remove pollutants from soil and concentrate them in harvestable part. This phytoremediation is possible because soil organisms increase the heavy metal solubility (Lone et al., 2008). Strong retention is observed in some plants, such as white lupin roots for cadmium pollution, while translocation occurs in wheat (Page et al., 2006). The translocation process may be due to a response of plants that recognize cadmium as a toxic compound. This leads to the activation of defense mechanisms (sequestration in the vacuole or in the cell walls). Plants can then be harvested and materials can be incinerated. Second, phyto-stabilization may be achieved through a suitable zone that plants provide around their roots. In this case, pollutants are stabilized and immobilized by roots that use different mechanisms, such as the production of specific substances, to render heavy metals harmless (Orgiazzi et al., 2016).

4.3.2.5. Climate warming mitigation

Climate change is one of the most important challenges that humans will have to face in the next decades (Orgiazzi et al., 2016). By creating large pores and tunnels, earthworms influence gas permeability and the activity of the microbiota responsible for the natural emission of greenhouse gases (CH_4 and N_2O). Through heterotrophic respiration, earthworms release CO_2, but reduced-tillage practices support the activities of earthworms and then promote C sequestration and N cycling in soils. Storage of C also increases through the conversion of croplands into permanent pastures and the management of plant diversity. Plants also have an impact on the C cycle by converting CO_2 and light energy into chemical energy (sugars). However, the release of CO_2 into the atmosphere is currently higher than fluxes into C sinks, leading to an unbalanced global C budget. Concerning the N cycle, chemical engineers such as bacteria convert the organic N into mineral forms that may be absorbed by plants. Earthworms also influence the N cycle by their structures particularly rich in nutrients and then become preferred sites for a number of soil processes, such as N fixation (Orgiazzi et al., 2016). Both earthworms and plants are part of complex interactions that lead to the decomposition of organic matter, releasing C and N in the soil. They are consequently crucial to biogeochemical cycles and therefore to the regulation of atmospheric composition and climate.

ESs are needed because they meet a human need. However, this vision remains an anthropocentric concept of ESs, and relatively few studies specify how and what human needs are potentially and actually fulfilled by ESs, particularly by ecosystem engineer services. The contribution of earthworms and plants to soil services is now clearly proven. However, further investigations are needed. For example, Bertrand et al. (2015) noted that the impact of pesticides on earthworms was not completely understood because of lack of field data on the exposure of earthworms to currently used molecules. Additional long-term field studies are essential to understanding the impact of earthworms on crop production (Bertrand et al., 2015). Moreover, major gaps remain in understanding the identification of all the ESs provided by each ecological group of earthworms to other soil biota. Finally, a cost-benefit analysis to assess the monetary values generated by earthworm populations at local or regional scale for economic evaluation should be taken into consideration (Sharma et al., 2017).

4.4. CONCLUSIONS AND FUTURE PROSPECTS

Ecosystem engineers, especially plants and earthworms, are strongly involved in pedogenesis and ecosystem functions. Their bioturbation activities as autogenic and allogenic engineers are at the core of humipedon formation and dynamics, with wide-reaching consequences on provisioning and regulating services at the ecosystem level. Soils as habitats for ecosystem engineers constitute an environment of high spatial and temporal heterogeneity, both in terms of physical properties as well as biological activities. This creates complex interactions, resulting in hotspots and hot moments. The understanding of these temporal and spatial processes is in its infancy. Gaps of knowledge still exist regarding the relationships between soil food webs and engineering processes. In this way, Sanders et al. (2014) underlined that ecosystem engineering species constitute potentially the most important bridges between trophic and nontrophic interactions. Therefore, there is considerable potential for advancing our understanding of engineer and food web dynamics areas via their integration. This approach is crucial to improve our knowledge about soil management in order to better predict the impact of changes in human practices and/or climate warming on ecosystem services.

REFERENCES

Alexandrovskiy, A. L. (2007). Rates of soil-forming processes in three main models of pedogenesis. *Revista Mexicana de Ciencias Geologicas*, *24*(2), 283–292. http://www.scielo.org.mx/scielo.php?script=sci_arttext&pid=S1026-87742007000200014&lng=es&nrm=iso

Amossé, J., Le Bayon, R. C., & Gobat, J.-M. (2015). Are urban soils similar to natural soils of river valleys? *Journal of Soils and Sediments*, *15*(8), 1716–1724. https://doi.org/10.1007/s11368-014-0973-6

Amossé, J., Turberg, P., Kohler-Milleret, R., Gobat, J.-M., & Le Bayon, R. C. (2015). Effects of endogeic earthworms on the soil organic matter dynamics and the soil structure in urban and alluvial soil materials. *Geoderma*, *243–244*, 50–57. https://doi.org/10.1016/j.geoderma.2014.12.007

Angers, D. A., & Caron J. (1998). Plant induced changes in soil structure processes and feedbacks. *Biogeochemistry*, *42*, 55–72. https://doi.org/10.1023/A:1005944025343

Bais, H. P., Weir, T. L., Perry, L. G., Gilroy, S., & Vivanco, J. M. (2006). The role of root exudates in rhizosphere interactions with plants and other organisms. *Annual Review of Plant Biology*, *57*(1), 233–266. https://doi.org/10.1146/annurev.arplant.57.032905.105159

Bardgett, R.D. (2005). *The biology of soil: A community and ecosystem approach*. Oxford and New York: Oxford University Press.

Barois, I., Villemin, G., Lavelle, P., & Toutain, F. (1993). Transformation of soil structure through *Pontoscolex corethrurus* (Oligochaeta) intestinal tract. *Geoderma*, *56*, 57–66. https://doi.org/10.1016/0016-7061(93)90100-Y

Bastardie, F., Capowiez, Y., & Cluzeau, D. (2005). 3D characterisation of earthworm burrow systems in natural soil cores collected from a 12-year-old pasture. *Applied Soil Ecology*, *30*, 34–46. https://doi.org/10.1016/j.apsoil.2005.01.001

Beare, M. H., Coleman, D. C., Crossley, D. A., Hendrix, P. F., & Odum, E. P. (1995). A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. *Plant and Soil*, *170*(1): 5–22.

Bengtson, P., Barker, J., & Grayston, S.J. (2012). Evidence of a strong coupling between root exudation, C and N availability, and stimulated SOM decomposition caused by rhizosphere priming effects. *Ecology and Evolution*, *2*, 1843–1852. https://doi.org/10.1002/ece3.311

Berendsen, R. L., Pieterse, C. M. J., & Bakker, P. A. H. M. (2012). The rhizosphere microbiome and plant health. *Trends in Plant Science*, *17*, 478–486. https://doi.org/10.1016/j.tplants.2012.04.001

Berke, S. K., Mahon, A. R., Lima, F. P., Halanych, K. M., Wethey, D. S., & Woodin, S. A. (2010). Range shifts and species diversity in marine ecosystem engineers: Patterns and predictions for European sedimentary habitats: Polychaete range shifts. *Global Ecology and Biogeography*, *19*(2), 223–232. https://doi.org/10.1111/j.1466-8238.2009.00509.x

Bertrand, M., Barot, S., Blouin, M., Whalen, J., de Oliveira, T. & Roger-Estrade, J. (2015). Earthworm services for cropping systems. A review. *Agronomy for Sustainable Development*, *35*(2), 553–567. https://doi.org/10.1007/s13593-014-0269-7

Binet, F., & Le Bayon, R. C. (1998). Space-time dynamics in situ of earthworm casts under temperate cultivated soils. *Soil Biology and Biochemistry*, *31*(1), 85–93. https://doi.org/10.1016/S0038-0717(98)00109-6

Bityutskii, N. P., Maiorov, E. I., & Orlova, N. E. (2012). The priming effects induced by earthworm mucus on mineralization and humification of plant residues. *European Journal of Soil Biology*, *50*, 1–6. https://doi.org/10.1016/j.ejsobi.2011.11.008

Blanchart, E., Albrecht, A., Alegre, J., Duboisset, A., Villenave, C., et al. (1999). Effects of earthworms on soil structure and physical properties. In: P. Lavelle, L. Brussard, & J. Hendrix (Eds.), *Earthworm management in tropical agrogroecosystems* (pp. 149–172). London: CAB International.

Blanchart, E., Bruand, A., & Lavelle, P. (1993). The physical structure of casts of *Millsonia anomala* (Oligochaeta: Megascolecidae) in shrub savanna soil (Côte d'Ivoire). *Geoderma*, *56*, 119–132. https://doi.org/10.1016/0016-7061(93)90104-S

Blanchart, E., Lavelle, P., Braudeau, E., Le Bissonnais, Y., & Valentin, C. (1997). Regulation of soil structure by geophagous earthworm activities in humid savannas of Côte d'Ivoire. *Soil Biology and Biochemistry*, *29*(3–4), 431–439. https://doi.org/10.1016/S0038-0717(96)00042-9

Blankinship, J. C., Fonte, S. J., Six, J., & Schimel, J. P. (2016). Plant versus microbial controls on soil aggregate stability in a seasonally dry ecosystem. *Geoderma*, *272*, 39–50. https://doi.org/10.1016/j.geoderma.2016.03.008

Blouin, M., Hodson, M. E., Delgado, E. A., Baker, G., Brussaard, L., Butt, K. R., et al. (2013). A review of earthworm impact on soil function and ecosystem services: Earthworm impact on ecosystem services. *European Journal of Soil Science*, *64*(2), 161–182. https://doi.org/10.1111/ejss.12025

Blouin, M., Sery, N., Cluzeau, D., Brun, J.-J., & Bédécarrats, A. (2013). Balkanized research in ecological engineering revealed by a bibliometric analysis of earthworms and ecosystem services. *Environmental Management*, *52*(2), 309–320. https://doi.org/10.1007/s00267-013-0079-8

Blouin, M., Zuily-Fodil, Y., Pham-Thi, A.-T., Laffray, D., Reversat, G., Pando, A., et al. (2005). Belowground organism activities affect plant aboveground phenotype, inducing plant tolerance to parasites. *Ecology Letters*, *8*(2), 202–208. https://doi.org/10.1111/j.1461-0248.2004.00711.x

Blum, W., Schad, P., & Nortcliff, S. (2018). *Essentials of soil science: Soil formation, functions,use and classification (World Reference Base)*. Borntrager Science Publishers.

Bodner, G., Leitner, D., & Kaul, H.-P. (2014). Coarse and fine root plants affect pore size distributions differently. *Plant and Soil*, *380*, 133–151. https://doi.org/10.1007/s11104-014-2079-8

Bottinelli, N., Henry-des-Tureaux, T., Hallaire, V., Mathieu, J., Benard, Y., Duc Tran, T., et al. (2010). Earthworms accelerate soil porosity turnover under watering conditions. *Geoderma*, *156*, 43–47. https://doi.org/10.1016/j.geoderma.2010.01.006

Bormann, B. T., Spaltenstein, H., McClellan, M. H., Ugolini, F. Cromack Jr., K. C., & Nay, S. M. (1995). Rapid soil development after wind throw disturbance in Pristine forests. *The Journal of Ecology*, *83*(5), 747. https://doi.org/10.2307/2261411

Bouché, M. B. (1977). Stratégies lombriciennes. In: U. Lohm & T. Person (Eds.), *Soil organisms as components of ecosystems.* Ecological Bulletins no. 25 (pp. 122–132). Stockholm: Swedish Natural Science Research Council.

Bouché, M. B. (1981). Contribution des lombriciens aux migrations d'éléments dans les sols tempérés. *Colloques Internationaux du Centre National de Recherche Scientifique*, *303*, 145–153.

Bowsher, A. W., Evans, S., Tiemann, L. K., & Friesen, M. L. (2018). Effects of soil nitrogen availability on rhizodeposition in plants: A review. *Plant and Soil*, *423*(1), 59–85. https://doi.org/10.1007/s11104-017-3497-1

Briat, J.-F., & Job, D. (2017). *Les sols et la vie souterraine: Des enjeux majeurs en agroécologie*. Quae.

Brown, G. G., Barois, I., & Lavelle, P. (2000). Regulation of soil organic matter dynamics and microbial activity in the drilosphere and the role of interactions with other edaphic functional domains. *European Journal of Soil Biology*, *36*(3–4), 177–198. https://doi.org/10.1016/S1164-5563(00)01062-1

Bruand, A., Cousin, I., Nicoullaud, B., Duval, O., & Begon, J. C. (1996). Backscattered electron scanning images of soil porosity for analysing soil compaction around roots. *Soil Science Society of America Journal*, *60*, 895–901. doi:10.2136/sssaj1996.03615995006000030031x

Bullinger-Weber, G., Guenat, C., Salomé, C., Gobat, J.-M., & Le Bayon, R. C. (2012). Impact of flood deposits on earthworm communities in alder forests from a subalpine floodplain (Kandersteg, Switzerland). *European Journal of Soil Biology*, *49*, 5–11. https://doi.org/10.1016/j.ejsobi.2011.08.001

Bullinger-Weber, G., Le Bayon, R. C., Guenat, C., & Gobat, J.-M. (2007). Influence of some physicochemical and biological parameters on soil structure formation in alluvial soils. *European Journal of Soil Biology*, *43*(1), 57–70. https://doi.org/10.1016/j.ejsobi.2006.05.003

Cameron, E. K., Cahill, J. F., & Bayne, E. M. (2014). Root foraging influences plant growth responses to earthworm foraging. *PLoS One*, *9*, e108873. https://doi.org/10.1371/journal.pone.0108873

Cameron, E. K., Proctor, H. C., & Bayne, E. M. (2013). Effects of an ecosystem engineer on belowground movement of microarthropods. *PLoS ONE*, *8*(4), e62796. https://doi.org/10.1371/journal.pone.0062796

Canti, M. G., & Piearce, T. G. (2003). Morphology and dynamics of calcium carbonate granules produced by different earthworm species: The 7th international symposium on earthworm ecology, Cardiff, Wales, 2002. *Pedobiologia*, *47*(5–6), 511–521. https://doi.org/10.1078/0031-4056-00221

Capowiez, Y., Bottinelli, N., Sammartino, S., Michel, E., & Jouquet, P. (2015). Morphological and functional characterisation of the burrow systems of six earthworm species (Lumbricidae). *Biology and Fertility of Soils*, *51*(7), 869–877. https://doi.org/10.1007/s00374-015-1036-x

Capowiez, Y., Sammartino, S., & Michel, E. (2014). Burrow systems of endogeic earthworms: Effects of earthworm abundance and consequences for soil water infiltration. *Pedobiologia*, *57*(4–6), 303–309. https://doi.org/10.1016/j.pedobi.2014.04.001

Carpenter, D., Hodson, M. E., Eggleton, P., & Kirk, C. (2007). Earthworm induced mineral weathering: Preliminary results. *European Journal of Soil Biology*, *43*, S176–S183. https://doi.org/10.1016/j.ejsobi.2007.08.053

Chapuis-Lardy, L., Le Bayon, R. C., Brossard, M., López-Hernández, D., & Blanchart, E. (2011). Role of soil macrofauna in phosphorus cycling. In E. Bünemann, A. Oberson, & E. Frossard (Eds.), *Phosphorus in Action* (Vol. 26, pp. 199–213). https://doi.org/10.1007/978-3-642-15271-9_8

Churchman, G. J. (2010). The philosophical status of soil science. *Geoderma*, *157*(3–4), 214–221. https://doi.org/10.1016/j.geoderma.2010.04.018

Chauvel, A., Grimaldi, M., Barros, E., Blanchart, E., Desjardins, T., Sarrazin, M., et al. (1999). Pasture damage by an Amazonian earthworm. *Nature*, *398*, 32–33.

Coleman, D. C., Crossley, D. A., & Hendrix, P. F. (2004). *Fundamentals of soil ecology*, 2nd ed. San Diego: Academic Press.

Cortez, J., & Bouché, M. (1987). Composition chimique du mucus cutané de *Allolobophora chaetophora chaetophora* (Oligochaeta: Lumbricidae). *Compte Rendu de l'Académie des Sciences de Paris, Série III*, *305*, 207–210.

Coyle, D. R., Nagendra, U. J., Taylor, M. K., Campbell, J. H., Cunard, C. E., Joslin, A. H., et al. (2017). Soil fauna responses to natural disturbances, invasive species, and global climate change: Current state of the science and a call to action. *Soil Biology and Biochemistry*, *110*, 116–133. https://doi.org/10.1016/j.soilbio.2017.03.008

Cunha, L., Brown, G. G., Stanton, D. W. G., Da Silva, E., Hansel, F. A., Jorge, G., et al. (2016). Soil animals and pedogenesis: The role of earthworms in anthropogenic soils. *Soil Science*, *181*(3/4), 110–125. https://doi.org/10.1097/SS.0000000000000144

Curry, J., & Schmidt, O. (2007). The feeding ecology of earthworms—a review. *Pedobiologia*, *50*, 463–477. http://dx.doi.org/10.1016/j.pedobi.2006.09.001

Cushman, J., Waller, J. C., & Hoak, D. R. (2010). Shrubs as ecosystem engineers in a coastal dune: Influences on plant populations, communities and ecosystems. *Journal of Vegetation Science*, *21*(5), 821–831. https://doi.org/10.1111/j.1654-1103.2010.01196.x

Darwin, C. R. (1881). *The formation of vegetable mould through the action of worms with observations on their habits*. London: Murray.

da Silva, R. T., Fleskens, L., van Delden, H., & van der Ploeg, M. (2018). Incorporating soil ecosystem services into urban planning: Status, challenges and opportunities. *Landscape Ecology*, *33*(7), 1087–1102. https://doi.org/10.1007/s10980-018-0652-x

Decaëns, T. (2000). Degradation dynamics of surface earthworm casts in grasslands of the eastern plains of Colombia. *Biology and Fertiity of Soils*, *32*(2), 149–156. https://doi.org/10.1007/s003740000229

Degens, B. P. (1997). Macro-aggregation of soils by biological bonding and binding mechanisms and the factors affecting these: A review. *Soil Research*, *35*, 431–460. https://doi.org/10.1071/S96016

Dominati, E., Patterson, M., & Mackay, A. (2010). A framework for classifying and quantifying the natural capital and ecosystem services of soils. *Ecological Economics*, *69*(9), 1858–1868. https://doi.org/10.1016/j.ecolecon.2010.05.002

Edwards, C. A. (2004). *Earthworm ecology*, 2nd ed. Boca Raton, FL: CRC Press, St. Lucie Press.

Edwards, C. A., & Bohlen, P. J. (1996). *The biology and ecology of earthworms*. London: Chapman and Hall.

Eisenhauer, N. (2010). The action of an animal ecosystem engineer: Identification of the main mechanisms of earthworm impacts on soil microarthropods. *Pedobiologia*, *53*(6), 343–352. https://doi.org/10.1016/j.pedobi.2010.04.003

Evans A. C. (1948). The identity of earthworms stored by moles. *Proceedings of the Zoological Society of London*, *118* (2), 356–359. https://doi.org/10.1111/j.1096-3642.1948.tb00381.x

FAO (2015). Revised World Soil Charter: 10.

Feeney, D. S., Crawford, J. W., Daniell, T., Hallett, P. D., Nunan, N., Ritz, K., et al. (2006). Three-dimensional microorganization of the soil–root–microbe system. *Microbial Ecology*, *52*(1), 151–158. https://doi.org/10.1007/s00248-006-9062-8

Feller, C., Brown, G. G., Blanchart, E., Deleporte, P., & Chernyanskii, S. S. (2003). Charles Darwin, earthworms and the natural sciences: Various lessons from past to future. *Agriculture, Ecosystems & Environment*, *99*(1–3), 29–49. https://doi.org/10.1016/S0167-8809(03)00143-9

Felten, D., & Emmerling, C. (2009). Earthworm burrowing behaviour in 2D terraria with single- and multi-species assemblages. *Biology and Fertility of Soils*, *45*, 789–797. https://doi.org/10.1007/s00374-009-0393-8

Finzi A., Abramoff, R.Z., Iller, K. S., Brzostek, E. R., Darby, B. A., Kramer, M. A., et al. (2015). Rhizosphere processes are quantitatively important components of terrestrial carbon and nutrient cycles. *Global Change Biology*, *21*, 2082–2094. https://doi.org/10.1111/gcb.12816

Fischer, C., Roscher, C., Jensen, B., Eisenhauer, N., Baade, J., Attinger, S., et al. (2014). How do earthworms, soil texture and plant composition affect infiltration along an experimental plant diversity gradient in grassland? *Plos One*, *9*(6), e98987. https://doi.org/10.1371/journal.pone.0098987

Fonte, S. J., Botero, C., Quintero, D. C., Lavelle, P., & van Kessel, C. (2019). Earthworms regulate plant productivity and the efficacy of soil fertility amendments in acid soils of the Colombian Llanos. *Soil Biology and Biochemistry*, *129*, 136–143. https://doi.org/10.1016/j.soilbio.2018.11.016

Fonte, S. J., Quintero, D. C., Velásquez, E., & Lavelle, P. (2012). Interactive effects of plants and earthworms on the physical stabilization of soil organic matter in aggregates. *Plant and Soil*, *359*(1–2), 205–214. https://doi.org/10.1007/s11104-012-1199-2

Forey, E., Chauvat, M., Coulibaly, S. F. M., Langlois, E., Barot, S., & Clause, J. (2018). Inoculation of an ecosystem engineer (Earthworm: *Lumbricus terrestris*) during experimental grassland restoration: Consequences for above and belowground soil compartments. *Applied Soil Ecology*, *125*, 148–155. https://doi.org/10.1016/j.apsoil.2017.12.021

Foster, R. C. (1998). Microenvironments of soil organisms. *Biology and Fertility of Soils*, *6*, 89–203. https://doi.org/10.1007/BF00260816

Frouz, J., Holec, M., & Kalcík, J. (2003). The effect of *Lasius niger* (Hymenoptera, Formicidae) ant nest on selected soil chemical properties. *Pedobiologia*, *47*, 205–212. https://doi.org/10.1016/j.geoderma.2015.10.022https://doi.org/10.1078/0031-4056-00184

Gabet, E. J., Reichman, O. J., & Seabloom, E. W. (2003). The effects of bioturbation on soil processes and sediment transport. *Annual Review of Earth and Planetary Sciences*, *31*(1), 249–273. https://doi.org/10.1146/annurev.earth.31.100901.141314

Ge, F., Shuster, W. D., Edwards, C. A., Parmelee, R. W., & Subler, S. (2001). Water stability of earthworm casts in manure- and inorganic-fertilizer amended agroecosystems influenced by age and depth. *Pedobiologia*, *45*, 12–26. https://doi.org/10.1078/0031-4056-00064

Gianfreda, L. (2015). Enzymes of importance to rhizosphere processes. *Journal of Soil Science and Plant Nutrition*, *15*(2), 283–306. http://dx.doi.org/10.4067/S0718-95162015005000022

Gianinazzi, S., Gollotte, A., Binet, M.-N., van Tuinen, D., Redecker, D., & Wipf, D. (2010). Agroecology: The key role of arbuscular mycorrhizas in ecosystem services. *Mycorrhiza*, *20*(8), 519–530. https://doi.org/10.1007/s00572-010-0333-3

Gilad, E., von Hardenberg, J., Provenzale, A., Shachake, M., & Meron, E. (2007). A mathematical model of plants as ecosystem engineers. *Journal of Theoretical Biology*, *244*, 680–691. https://doi.org/10.1016/j.jtbi.2006.08.006

Gobat, J. M., & Le Bayon, R. C. (2013). Structures des sols et êtres vivants. In *Les sols et leurs structures: Observations à différentes échelles* (pp. 39–62). Paris: QUAE Editions, INRA.

Grigoropoulou, N., & Butt, K. R. (2012). Assessment of burrow re-use by *Lumbricus terrestris* L. through field experimentation. *Zeszyty Naukowe*, *15*, 43–51.

Guderle, M., & Hildebrandt, A. (2015). Using measured soil water contents to estimate evapotranspiration and root water uptake profiles: A comparative study. *Hydrology and Earth System Sciences*, *19*(1), 409–425. https://doi.org/10.5194/hess-19-409-2015

Guéi, A. M., Baidai, Y., Tondoh, J. E., & Huising, J. (2012). Functional attributes: Compacting vs decompacting earthworms and influence on soil structure. *Current Zoology*, *58*(4), 556–565. https://doi.org/10.1093/czoolo/58.4.556

Guggenberger, G., Thomas, R.J., & Zech, W. (1996). Soil organic matter within earthworm casts of an anecicendogeic tropical pasture community, Columbia. *Applied Soil Ecology*, *3*, 263–274. https://doi.org/10.1016/0929-1393(95)00081-X

Gurnell, A., & Petts, G. (2006). Trees as riparian engineers: The Tagliamento river, Italy. *Earth Surface Processes and Landforms*, *31*(12), 1558–1574. https://doi.org/10.1002/esp.1342

Gutiérrez, J. L., & Jones, C. G. (2006). Physical ecosystem engineers as agents of biogeochemical heterogeneity. *BioScience*, *56*, 227–236. https://doi.org/10.1641/0006-3568(2006)056[0227:PEEAAO]2.0.CO;2

Hirth, J. R., McKenzie, B. M., & Tisdall, J. M. (1998). Roots of perennial ryegrass (*Lolium perenne*) influence the burrowing of the endogeic earthworm, *Apporrectodea rosea*. *Soil Biology and Biochemistry*, *14*, 2181–2183. https://doi.org/10.1016/S0038-0717(98)00074-1

Hoang, D. T. T., Razavi, B. S., Kuzyakov, Y., & Blagodatskaya, E. (2016). Earthworm burrows: Kinetics and spatial distribution of enzymes of C-, N- and P- cycles. *Soil Biology and Biochemistry*, *99*, 94–103. https://doi.org/10.1016/j.soilbio.2016.04.021

Hodson, M. E., Black, S., Brinza, L., Carpenter, D., Lambkin, D. C., Mosselmans, J. F. W., et al. (2014). Biology as an agent of chemical and mineralogical change in soil. *Procedia Earth and Planetary Science*, *10*, 114–117. https://doi.org/10.1016/j.proeps.2014.08.039

Horn, R., & Smucker, A. (2005). Structure formation and its consequences for gas and water transport in unsaturated arable and forest soils. *Soil and Tillage Research*, *82*(1), 5–14. https://doi.org/10.1016/j.still.2005.01.002

Huang, X.-F., Chaparro, J. M., Reardon, K., F., Zhang, R., Shen, Q., & Vivanco J. M. (2014). Rhizosphere interactions: Root exudates, microbes, and microbial communities. *Botany*, *92*, 267–275. https://doi.org/10.1139/cjb-2013-0225

Ings, T. C., Montoya, J. M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C. F., et al. (2009). Review: Ecological networks - beyond food webs. *Journal of Animal Ecology*, *78*(1), 253–269. https://doi.org/10.1111/j.1365-2656.2008.01460.x

Jackson, L. E., Burger, M., & Cavagnaro, T. R. (2008). Roots, nitrogen transformations, and ecosystem services. *Annual Review of Plant Biology*, *59*(1), 341–363. https://doi.org/10.1146/annurev.arplant.59.032607.092932

Javaux, M., Couvreur, V., Vanderborght, J., & Vereecken, H. (2013). Root water uptake: From three-dimensional biophysical processes to macroscopic modeling approaches. *Vadose Zone Journal*, *12*(4). https://doi.org/10.2136/vzj2013.02.0042

Jégou, D., Cluzeau, D., Balesdent, J., & Tréhen, P. (1998). Effects of four ecological categories of earthworms on carbon transfer in soil. *Applied Soil Ecology*, *9*, 249–255. https://doi.org/10.1016/S0929-1393(97)00057-7

Johnson-Maynard, J. L., Graham, R. C., Wu, L., & Shouse, P. J. (2002). Modification of soil structural and hydraulic properties after 50 years of imposed chaparral and pine vegetation. *Geoderma*, *110*, 227–240. https://doi.org/10.1016/S0016-7061(02)00232-X

Johnson-Maynard, J. L., & Strawn, D. G. (2016). Linking physical and biogeochemical properties and processes in the drilosphere. *Soil Science*, *181*, 126–132. doi: 10.1097/SS.0000000000000142

Johnson-Maynard, J. L., Umiker, K. J., & Guy, S. O. (2007). Earthworm dynamics and soil physical properties in the first three years of no-till management. *Soil and Tillage Research*, *94*, 338–345. https://doi.org/10.1016/j.still.2006.08.011

Jones, C. G., Gutiérrez, J. L., Byers, J. E., Crooks, J. A., Lambrinos, J. G., & Talley, T. S. (2010). A framework for understanding physical ecosystem engineering by organisms.

Oikos, *119*(12), 1862–1869. https://doi.org/10.1111/j.1600-0706.2010.18782.x

Jones, C. G, Lawton J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, *69*, 373–386. doi: 10.2307/3545850.

Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, *78*(7), 1946–1957. https://doi.org/10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2

Jones, D. L., Nguyen, C., & Finlay, R. D. (2009). Carbon flow in the rhizosphere: Carbon trading at the soil-root interface. *Plant and Soil*, *321*, 5–33. https://doi.org/ 10.1007/s11104-009-9925-0

Jouquet, P., Blanchart, E., & Capowiez, Y. (2014). Utilization of earthworms and termites for the restoration ecosystem functioning. *Applied Soil Ecology*, *73*, 34–40. https://doi.org/10.1016/j.apsoil.2013.08.004

Jouquet, P., Chaudhary, E., & Kumar, A. R. V. (2018). Sustainable use of termite activity in agro-ecosystems with reference to earthworms. A review. *Agronomy for Sustainable Development*, *38*(1). https://doi.org/10.1007/s13593-017-0483-1

Kanianska, R., Jadudová, J., Makovníková, J., Kizeková, M. (2016). Assessment of relationships between earthworms and soil abiotic and biotic factors as a tool in sustainable agricultural. *Sustainability*, *8*, 1–14. https://doi.org/10.3390/su8090906

Kim, Y. N., Robinson, B., Lee, K. A., Boyer, S., & Dickinsona, N. (2017). Interactions between earthworm burrowing, growth of a leguminous shrub and nitrogen cycling in a former agricultural soil. *Applied Soil Ecology*, *110*, 79–87. https://doi.org/10.1016/j.apsoil.2016.10.011

Knight, D., Elliott, P. W., Anderson, J. M., & Scholefield, D. (1992). The role of earthworms in managed, permanent pastures in Devon. *Engl. Soil Biology and Biochemistry*, *24*, 1511–1517. https://doi.org/10.1016/0038-0717(92)90142-K

Kooch, Y., Darabi, S. M., & Hosseini, S. M. (2015). Effects of pits and mounds following windthrow events on soil features and greenhouse gas fluxes in a temperate forest. *Pedosphere*, *25*(6), 853–867. https://doi.org/10.1016/S1002-0160(15)30066-7

Kooch, Y., Hosseini, S. M., Samonil, P., & Hojjati, S. M. (2014). The effect of windthrow disturbances on biochemical and chemical soil properties in the northern mountainous forests of Iran. *Catena*, *116*, 142–148. https://doi.org/10.1016/j.catena.2014.01.002

Kooch, Y., Zaccone, C., Lamersdorf, N. P., & Tonon, G. (2014). Pit and mound influence on soil features in an oriental beech (Fagus orientalis Lipsky) forest. *European Journal of Forest Research*, *133*(2), 347–354. https://doi.org/10.1007/s10342-013-0766-2

Kuzyakov, Y., & Blagodatskaya, E. (2015). Microbial hotspots and hot moments in soil: Concept and review. *Soil Biology and Biochemistry*, *83*, 184–199. https://doi.org/10.1016/j.soilbio.2015.01.025

Lambkin, D. C., Gwilliam, K. H., Layton, C., Canti, M. G., Piearce, T. G., & Hodson, M. E. (2011). Production and dissolution rates of earthworm-secreted calcium carbonate. *Pedobiologia*, *54*, S119–S129. https://doi.org/10.1016/j.pedobi.2011.09.003

Landeweert, R., Hoffland, E., Finlay, R. D., Kuyper, T. W., & van Breemen, N. (2001). Linking plants to rocks: Ectomycorrhizal fungi mobilize nutrients from minerals. *Trends in Ecology & Evolution*, *16*(5), 248–254. https://doi.org/10.1016/S0169-5347(01)02122-X

Lavelle, P. (1988). Earthworm activities and the soil system. *Biology and Fertility of Soils*, *6*, 237–251. https://doi.org/10.1007/BF00260820

Lavelle, P., Bignell, D., Lepage, M., Wolters, V., Roger, P., Ineson, P., et al. (1997). Soil function in a changing world: The role of invertebrate ecosystem engineers. *European Journal of Soil Biology (France)*. Retrieved from http://agris.fao.org/agris-search/search.do?recordID=FR1999003405

Lavelle, P., & Spain, A. V. (2001). *Soil ecology*. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Lavelle, P., Spain, A., Blouin, M., Brown, G., Decaëns, T., Grimaldi, M., et al. (2016). Ecosystem engineers in a self-organized soil: A review of concepts and future research questions. *Soil Science*, *181*(3/4), 91–109. https://doi.org/10.1097/SS.0000000000000155

Le Bayon, R. C., & Binet, F. (1999). Rainfall effects on erosion of earthworm casts and phosphorus transfers by water runoff. *Biology and Fertility of Soils*, *30*(1–2), 7–13. https://doi.org/10.1007/s003740050580

Le Bayon, R. C., & Binet, F. (2001). Earthworm surface casts affect soil erosion by runoff water and phosphorus transfer in a temperate maize crop. *Pedobiologia*, *45*(5), 430–442. https://doi.org/10.1078/0031-4056-00097

Le Bayon, R. C., & Binet, F. (2006). Earthworms change the distribution and availability of phosphorous in organic substrates. *Soil Biology and Biochemistry*, *38*(2), 235–246. https://doi.org/10.1016/j.soilbio.2005.05.013

Le Bayon, R. C., Bullinger-Weber, G., Schomburg, A. C., Turberg, P., Schlaepfer, R., & Guenat, C. (2017). Earthworms as ecosystem engineers: A review. In C. G. Horton (Ed.), *Earthworms: Types, roles and research* (pp. 129–178). New York: NOVA Science Publishers.

Le Bayon, R. C., & Milleret, R. (2009). Effects of earthworms on phosphorus dynamics – A review. *Dynamic Soil, Dynamic Plant*, *3*, 21–27.

Le Bayon, R. C., Moreau, S., Gascuel-Odoux, C., & Binet, F. (2002). Annual variations in earthworm surface-casting activity and soil transport by water runoff under a temperate maize agroecosytem. *Geoderma*, *106*(1–2), 121–135. https://doi.org/10.1016/S0016-7061(01)00121-5

Lee, K.E., (1985). *Earthworms: Their ecology and relationships with soil and land use*. Sydney, Australia: Academic Press.

Lehmann, A., Zheng, W., & Rillig, M. C. (2017). Soil biota contributions to soil aggregation. *Nature Ecology & Evolution*, *1*(12), 1828–1835. https://doi.org/10.1038/s41559-017-0344-y

Lehmann, A., Leifheit, E. F., & Rillig, M. C. (2017). Mycorrhizas and soil aggregation. In *Mycorrhizal mediation of soil* (pp. 241–262). Elsevier. Retrieved from https://linkinghub.elsevier.com/retrieve/pii/B9780128043127000140

Lipiec, J., Siczek, A., Sochan, A., & Bieganowski, A. (2016). Effect of sand grain shape on root and shoot growth of wheat seedlings. *Geoderma*, *265*, 1–5. https://doi.org/10.1016/j.geoderma.2015.10.022

Liu, R., Zhu, F., Song, N., Yang, X., & Chai, Y. (2013) Seasonal distribution and diversity of ground arthropods in microhabitats following a shrub plantation age sequence in desertified steppe. *PLoS One*, *8*(10), e77962. https://doi.org/10.1371/journal.pone.0077962

Lone, M.I, He, Z.-L, Stoffella, P.J., Yang, X.-E. (2008). Phytoremediation of heavy metal polluted soils and water: Progresses and perspectives. *Journal of Zhejiang University SCIENCE B*, *9(3),* 210–220. https://link.springer.com/article/10.1631/jzus.B0710633

Lugtenberg, B., & Kamilova, F. (2009). Plant-growth-promoting rhizobacteria. *Annual Review in Microbiology*, *63*, 541–556. https://doi.org/ 10.1146/annurev.micro.62.081307.

Lynch, J. (1990). *The rhizosphere*. London: Wiley.

Marhan, S. & Scheu, S. (2005). The influence of mineral and organic fertilisers on the growth of the endogeic earthworm *Octolasion tyrtaeum* (Savigny). *Pedobiologia*, *49*, 239–249. https://doi.org/10.1016/j.pedobi.2004.11.002

Marinissen, J. C. Y. & Dexter, A. D. (1990). Mechanisms of stabilization of earthworm casts and artificial casts. *Biology and Fertility of Soils*, *9*, 163–167.

McKenzie, B. M., & Dexter, A. R. (1987). Physical properties of casts of the earthworm *Aporrectodea rosea*. *Biology and Fertility of Soils*, *5*, 152–157. https://doi.org/10.1007/BF00257651

MEA (2005). *Ecosystems and Human Well-being: Synthesis*. https://www.millenniumassessment.org/documents/document.356.aspx.pdf

Milcu, A., Schumacher, J., & Scheu, S. (2006). Earthworms (*Lumbricus terrestris*) affect plant seedling recruitment and microhabitat heterogeneity. *Functional Ecology*, *20*, 261–268. https://doi.org/10.1111/j.1365-2435.2006.01098.x

Milleret, R., Le Bayon, R. C., Lamy, F., Gobat, J.-M., & Boivin, P. (2009). Impact of roots, mycorrhizas and earthworms on soil physical properties as assessed by shrinkage analysis. *Journal of Hydrology*, *373*(3–4), 499–507. https://doi.org/10.1016/j.jhydrol.2009.05.013

Milleret, R., Le Bayon, R. C., & Gobat, J.-M. (2009). Root, mycorrhiza and earthworm interactions: Their effects on soil structuring processes, plant and soil nutrient concentration and plant biomass. *Plant and Soil*, *316*(1–2), 1–12. https://doi.org/10.1007/s11104-008-9753-7

Mimmo, Y., Pii, F., Valentinuzzi, S., Astolfi, N., Lehto, B., Robinson, G., et al. (2018). Nutrient availability in the rhizosphere: A review. *Acta horticulturae*, *1217*, 13–28. https://doi.org/10.17660/ActaHortic.2018.1217.2

Mitchell, A. R., Ellsworth, T. R., & Meek, B. D. (1995). Effect of root systems on preferential flow in swelling soil. *Communications in Soil Science and Plant Analysis*, *26*(15–16), 2655–2666. https://doi.org/10.1080/00103629509369475

Mo, X., Qiao, Y., Sun, Z., Sun, X., & Li, Y. (2012). Molecular toxicity of earthworms induced by cadmium contaminated soil and biomarkers screening. *Journal of Environmental Sciences*, *24*(8), 1504–1510. https://doi.org/10.1016/S1001-0742(11)60957-1

Müller-Lemans, H., & van Dorp, F. (1996). Bioturbation as a mechanism for radionuclide transport in soil: Relevance of earthworms. *Journal of Environmental Radioactivity*, *31*(1), 7–20. https://doi.org/10.1016/0265-931X(95)00029-A

Nimmo, J. R. (2004). Porosity and pore size distribution. In D. Hillel (Ed.), *Encyclopedia of Soils in the Environment* (pp. 295–303). London, Elsevier.

Nuutinen, V. (2011). The meek shall inherit the burrow: Feedback in earthworm soil modification. In A. Karaca (Ed.), *Biology of earthworms* (pp. 123–140). Springer, Berlin.

Oades, J. M. (1993). The role of biology in the formation, stabilization and degradation of soil structure. In L. Brussaard & M. J. Kooistra (Eds.), *Soil structure/soil biota interrelationships* (pp. 377–400). Amsterdam: Elsevier. Retrieved from http://www.sciencedirect.com/science/article/pii/B9780444814906500339

Ojha, B., & Devkota, D. (2014). Earthworms: Soil and ecosystem engineers—A review. *World Journal of Agricultural Research*, *2*, 257–260. http://pubs.sciepub.com/wjar/2/6/1/

Orgiazzi, A., Bardgett, R. D., Barrios, E., Behan-Pelletier, V., Briones, M. J. I., Chotte, J.-L., et al. (2016). *Global soil biodiversity atlas*. Luxembourg: European Commission.

Page, V., Le Bayon, R. C. L., & Feller, U. (2006). Partitioning of zinc, cadmium, manganese and cobalt in wheat (*Triticum aestivum*) and lupin (*Lupinus albus*) and further release into the soil. *Environmental and Experimental Botany*, *58*(1–3), 269–278. https://doi.org/10.1016/j.envexpbot.2005.09.005

Paoletti, M. G. (1999). The role of earthworms for assessment of sustainability and as bioindicators. *Agriculture, Ecosystem and Environment*, *74*, 137–155. https://doi.org/10.1016/S0167-8809(99)00034-1

Parelho, C., Rodrigues, A. dos santos, Bernardo, F., do Carmo Barreto, M., Cunha, L., Poeta, P., & Garcia, P. (2018). Biological endpoints in earthworms (*Amynthas gracilis*) as tools for the ecotoxicity assessment of soils from livestock production systems. *Ecological Indicators*, *95*, 984–990. https://doi.org/10.1016/j.ecolind.2017.09.045

Pawlik, Ł., Phillips, J. D., & Šamonil, P. (2016). Roots, rock, and regolith: Biomechanical and biochemical weathering by trees and its impact on hillslopes—A critical literature review. *Earth-Science Reviews*, *159*, 142–159. https://doi.org/10.1016/j.earscirev.2016.06.002

Pelíšek, I. (2018). Investigation of soil water infiltration at a scale of individual earthworm channels. *Soil and Water Research*, *13 (2018)*(No. 1), 1–10. https://doi.org/10.17221/283/2014-SWR

Pérès, G., Bellido, A., Curmi, P., Marmonier, P., & Cluzeau, D. (2010). Relationships between earthworm communities and burrow numbers under different land use systems. *Pedobiologia*, *54*, 37–44. https://doi.org/10.1016/j.pedobi.2010.08.006

Pérès, G., Vandenbulcke, F., Guernion, M., Hedde, M., Beguiristain, T., Douay, F., et al. (2011). Earthworm indicators as tools for soil monitoring, characterization and risk assessment. An example from the national Bioindicator programme (France). *Pedobiologia*, *54*, S77–S87. https://doi.org/10.1016/j.pedobi.2011.09.015

Perreault, J.M., & Whalen, J.K. (2006). Earthworm burrowing in laboratory microcosms as influenced by soil temperature and moisture. *Pedobiologia*, *50*, 397–403.

Pierret, A., Doussan, C., Capowiez, Y., Bastardie, F., & Pagès, L. (2007). Root functional architecture: A framework for modeling the interplay between roots and soil. *Vadose Zone Journal*, *6*(2), 269–281. https://doi.org/10.2136/vzj2006.0067

Potvin L. R., & Lilleskov, E. A. (2017). Introduced earthworm species exhibited unique patterns of seasonal activity and vertical distribution, and *Lumbricus terrestris* burrows remained usable for at least 7 years in hardwood and pine stands. *Biology and Fertility of Soils*, *53*, 187–198. https://doi.org/10.1007/s00374-016-1173-x

Raaijmakers, J., Paulitz, T., Steinberg, C., Alabouvette, C., & Moënne-Loccoz, Y. (2009). The rhizosphere: A playground and battlefield for soilborne pathogens and beneficial microorganisms. *Plant and Soil*, *321*, 341–361. https://doi.org/10.1007/s11104-008-9568-6

Richter, D. D., Oh, N. H., Fimmen, R. & Jackson, J. (2007). The rhizosphere and soil formation. In: Z. G. Cardon, J. L. Whitbeck (Eds), *The rhizosphere: An ecological perspective* (pp. 179–200). New York: Academic Press.

Rossi, J. P. 2003. The spatiotemporal pattern of a tropical earthworm species assemblage and its relationship with soil structure. *Pedobiologia*, *47*, 497–503. https://doi.org/10.1078/0031-4056-00219

Salmon, S. (2001.) Earthworm excreta (mucus and urine) affect the distribution of springtails in forest soils. *Biology and Fertility of Soils*, *34*, 304–310. https://doi.org/10.1007/s003740100407

Salomé, C., Guenat, C., Bullinger-Weber, G., Gobat, J.-M., & Le Bayon, R. C. (2011). Earthworm communities in alluvial forests: Influence of altitude, vegetation stages and soil parameters. *Pedobiologia*, *54*, S89–S98. https://doi.org/10.1016/j.pedobi.2011.09.012https://doi.org/10.2136/vzj2017.01.0021

Šamonil, P., Daněk, P., Schaetzl, R. J., Vašíčková, I., & Valtera, M. (2015). Soil mixing and genesis as affected by tree uprooting in three temperate forests: Soil mixing and evolution as affected by tree-throw. *European Journal of Soil Science*, *66*(3), 589–603. https://doi.org/10.1111/ejss.12245

Šamonil, P., Král, K., & Hort, L. (2010). The role of tree uprooting in soil formation: A critical literature review. *Geoderma*, *157*(3–4), 65–79. https://doi.org/10.1016/j.geoderma.2010.03.018

Šamonil, P., Tejnecký, V., Borůvka, L., Šebková, B., Janík, D., & Šebek, O. (2010). The role of tree uprooting in Cambisol development. *Geoderma*, *159*(1–2), 83–98. https://doi.org/10.1016/j.geoderma.2010.06.020

Sanders, D., Jones, C.G., Thébault, E., Bouma, T. J., van der Heide, T., van Belzen, J., et al. (2014). Integrating ecosystem engineering and food webs. *Oikos*, *123*, 513–524. https://doi.org/10.1111/j.1600-0706.2013.01011.x

Savin, M. C., Görres, J. H., & Amador, J. A. (2004). Microbial and microfaunal community dynamics in artificial and *Lumbricus terrestris* (L.) burrows. *Soil Science Society of America Journal*, *68*, 116–124. doi:10.2136/sssaj2004.1160

Schaetzl, R. J., Burns, S. F., Small, T. W., & Johnson, D. L. (1990). Tree uprooting: Review of types and patterns of soil disturbance. *Physical Geography*, *11*(3), 277–291. https://doi.org/10.1080/02723646.1990.10642407

Schindler, S., O'Neill, F. H., Biró, M., Damm, C., Gasso, V., Kanka, R., et al. (2016). Multifunctional floodplain management and biodiversity effects: A knowledge synthesis for six European countries. *Biodiversity and Conservation*, *25*(7), 1349–1382. https://doi.org/10.1007/s10531-016-1129-3

Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A. et al. (2011). Persistence of soil organic matter as an ecosystem property. *Nature*, *478*(7367), 49–56.

Schomburg, A., Schilling, O. S., Guenat, C., Schirmer, M., Le Bayon, R. C., & Brunner, P. (2018). Topsoil structure stability in a restored floodplain: Impacts of fluctuating water levels, soil parameters and ecosystem engineers. *Science of the Total Environment*, *639*, 1610–1622. https://doi.org/10.1016/j.scitotenv.2018.05.120

Schomburg, A., Verrecchia, E. P., Guenat, C., Brunner, P., Sebag, D., & Le Bayon, R. C. (2018). Rock-Eval pyrolysis discriminates soil macro-aggregates formed by plants and earthworms. *Soil Biology and Biochemistry*, *117*, 117–124. https://doi.org/10.1016/j.soilbio.2017.11.010

Schrader, S., & Zhang, H. (1997). Earthworm casting: Stabilization or destabilization of soil structure? *Soil Biology and Biochemistry*, *29*, 469–475. https://doi.org/10.1016/S0038-0717(96)00103-4

Schulmann, O. P., & Tiunov, A. V. (1999). Leaf litter fragmentation by the earthworm *Lumbricus terrestris* L. *Pedobiologia*, *43*, 453–458.

Schulz, S., Brankatschk, R., Dümig, A., Kögel-Knabner, I., Schloter, M., & Zeyer, J. (2013). The role of microorganisms at different stages of ecosystem development for soil formation. *Biogeosciences*, *10*(6), 3983–3996. https://doi.org/10.5194/bg-10-3983-2013

Sharma, D. K., Tomar, S., & Chakraborty, D. (2017). Role of earthworm in improving soil structure and functioning. *Current Science*, *113*(6), 1064–1071.

Shipitalo, M., & Le Bayon, R. C. (2004). Quantifying the effects of earthworms on soil aggregation and porosity. In C. Edwards (Ed.), *Earthworm ecology* (pp. 183–200). https://doi.org/10.1201/9781420039719.pt5

Shipitalo, M. J., & Protz, R. (1988). Factors influencing the dispersibility of clay in worm casts, *Soil Science Society of America Journal*, *52*, 764–769. doi:10.2136/sssaj1988.03615995005200030030x

Shipitalo, M. J., & Protz, R. (1989). Chemistry and micromorphology of aggregation in earthworm casts. *Geoderma*, *45*, 357–374. https://doi.org/10.1016/0016-7061(89)90016-5

Six, J., Bossuyt, H., Degryze, S., & Denef, K. (2004). A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. *Soil and Tillage Research*, *79*(1), 7–31. https://doi.org/10.1016/j.still.2004.03.008

Six, J., Conant, R. T., Paul, E. A. & Paustian, K. (2002). Stabilization mechanisms of soil organic matter: Implication of C-saturation of soils. *Plant and Soil*, *241*, 155–176. https://doi.org/10.1023/A:1016125726789

Smith, P., Cotrufo, M. F., Rumpel, C., Paustian, K., Kuikman, P. J., Elliott, J. A., et al. (2015). Biogeochemical cycles and biodiversity as key drivers of ecosystem services provided by soils. *Soil*, *1*(2), 665–685. https://doi.org/10.5194/soil-1-665-2015

Stockdill, S. M. J. (1966). The effect of earthworms on pastures. *Proceedings of the New Zealand Ecological Society*, *13*, 68–75.

Suzuki, Y., Matsubara, T., & Hoshino, M. (2003). Breakdown of mineral grains by earthworms and beetle larvae. *Geoderma*, *112*(1), 131–142. https://doi.org/10.1016/S0016-7061(02)00300-2

Taylor, L. L., Leake, J. R., Quirk, J., Hardy, K., Banwart, S. A., & Beerling, D. J. (2009). Biological weathering and the long-term carbon cycle: Integrating mycorrhizal evolution and function into the current paradigm. *Geobiology*, *7*(2), 171–191. https://doi.org/10.1111/j.1472-4669.2009.00194.x

Teuling, A. J., Uijlenhoet, R., Hupet, F., & Troch, P. A. (2006). Impact of plant water uptake strategy on soil moisture and evapotranspiration dynamics during drydown. *Geophysical Research Letters*, *33*(3), 1–5. https://doi.org/10.1029/2005GL025019

Tisdall, J. M., & Oades J. M. (1982). Organic matter and water-stable aggregates in soils. *Journal of Soil Science*, *33*, 141–163. https://doi.org/10.1111/j.1365-2389.1982.tb01755.x

Tiunov, A. V., & Scheu S. (1999). Microbial respiration, biomass, biovolume and nutrient status in burrow walls of *Lumbricus terrestris* L. (Lumbricidae). *Soil Biology and Biochemistry*, *31*, 2039–2048. https://doi.org/10.1016/S0038-0717(99)00127-3

Topoliantz, S., Ponge, J. F., & Viaux, P. (2000). Earthworm and enchytraeid activity under different arable farming systems, as exemplified by biogenic structures. *Plant and Soil*, *225*, 39–51. https://doi.org/10.1023/A:1026537632468

Totsche, K. U., Amelung, W., Gerzabek, M. H., Guggenberger, G., Klumpp, E., Knief, C., et al. (2018). Microaggregates in soils. *Journal of Plant Nutrition and Soil Science*, *181*(1), 104–136. https://doi.org/10.1002/jpln.201600451

Trigo, D., Barois, I., Garvin, M. H., Huerta, E., Irisson, S., & Lavelle, P. (1999). Mutualism between earthworms and soil microflora. *Pedobiologia*, *43*(6), 866–873. https://www.jstor.org/stable/42947357

Uvarov, A. V., Tiunov, A. V., & Scheu, S. (2011). Effects of seasonal and diurnal temperature fluctuations on population dynamics of two epigeic earthworm species in forest soil. *Soil Biology and Biochemistry*, *43*, 559–570. https://doi.org/10.1016/j.soilbio.2010.11.023

Valtera, M., & Schaetzl, R. J. (2017). Pit-mound microrelief in forest soils: Review of implications for water retention and hydrologic modelling. *Forest Ecology and Management*, *393*, 40–51. https://doi.org/10.1016/j.foreco.2017.02.048

van Groenigen, J. W., Lubbers, I. M., Vos, H. M. J., Brown, G. G., De Deyn, G. B., & van Groenigen, K. J. (2014). Earthworms increase plant production: A meta-analysis. *Scientific Reports*, *4*, 6365. https://doi.org/10.1038/srep06365

van Groenigen, J. W., van Groenigen, K. J., Koopmans, G. F., Stokkermans, L., Vosa, H.M.J., & Lubbers, I. M. (2019). How fertile are earthworm casts? A meta-analysis. *Geoderma*, *338*, 525–535. https://doi.org/10.1016/j.geoderma.2018.11.001

Véle, A., Holuša, J., Frouz, J., & Konvička, O. (2011). Local and landscape drivers of ant and carabid beetle communities during spruce forest succession. *European Journal of Soil Biology*, *47*, 349–356. https://doi.org/10.1016/j.ejsobi.2011.09.003

Weil, R. R., & Brady, N. C. (2017). *The nature and properties of soils* (15th ed.). Essex, England: Pearson.

Weisskopf, L., Le Bayon, R. C., Kohler, F., Page, V., Jossi, M., Gobat, J.-M., et al. (2008). Spatio-temporal dynamics of bacterial communities associated with two plant species differing in organic acid secretion: A one-year microcosm study on lupin and wheat. *Soil Biology and Biochemistry*, *40*(7), 1772–1780. https://doi.org/10.1016/j.soilbio.2008.02.018

Whalen, J. K., Sampedro, L., & Waheed, T. (2004). Quantifying surface and subsurface cast production by earthworms under controlled laboratory conditions. *Biology and Fertility of Soils*, *39*, 287–291. https://doi.org/10.1007/s00374-003-0715-1

Wilkinson, M. T., Richards, P. J., & Humphreys, G. S. (2009). Breaking ground: Pedological, geological, and ecological implications of soil bioturbation. *Earth-Science Reviews*, *97*(1–4), 257–272. https://doi.org/10.1016/j.earscirev.2009.09.005

Wilson, G. W. T., Hartnett, D. C. & Rice, C. W. (2006). Mycorrhizal-mediated phosphorus transfer between the tallgrass prairie plants *Sorghastrum nutans* and *Artemisia ludoviciana*. *Functional Ecology*, *20*, 427–435. https://doi.org/10.1111/j.1365-2435.2006.01134.x

Wright, J. P., & Jones, C. G. (2006). The concept of organisms as ecosystem engineers ten years on: Progress, limitations, and challenges. *BioScience*, *56*(3), 203–209. https://doi.org/10.1641/0006-3568(2006)056[0203:TCOOAE]2.0.CO;2

Wu, H., Wang, X., & He, X. (2017). Effects of selected root exudate components on nitrogen removal and development of denitrifying bacteria in constructed wetlands. *Water*, *9*, 430. https://doi.org/10.3390/w9060430

Xu, H. J., Chen, H., Wang, X. L., Zhang, Y. L., Wang, J. J., Li, N. et al. (2018). Earthworms stimulate nitrogen transformation in an acidic soil under different Cd contamination. *Ecotoxicology and Environmental Safety*, *165*, 564–572. https://doi.org/10.1016/j.ecoenv.2018.09.042

Yunusa, I. A. M., & Newton, P. J. (2003). Plants for amelioration of subsoil constraints and hydrological control: The primer-plant concept. *Plant and Soil*, *257*, 261–281. http://www.jstor.org/stable/24124333.

Zanella, A., Ponge, J.-F., Jabiol, B., Sartori, G., Kolb, E., Gobat, J.-M., et al. (2018). Humusica 1, article 4: Terrestrial humus systems and forms—Specific terms and diagnostic horizons. *Applied Soil Ecology*, *122*, 56–74. https://doi.org/10.1016/j.apsoil.2017.07.005

Zangerlé, A., Renard, D., Iriarte, J., Suarez Jimenez, L. E., Adame Montoya, K. L., Juilleret, J., et al. (2016). The Surales, self-organized earth-mound landscapes made by earthworms in a seasonal tropical wetland. *Plos One*, *11*(5), e0154269. https://doi.org/10.1371/journal.pone.0154269

Zhang, D., Chen, Y., Ma, Y., Guo, L., Suna, J., & Tong, J. (2016). Earthworm epidermal mucus: Rheological behavior reveals drag-reducing characteristics in soil. *Soil and Tillage Research*, *158*, 57–66. https://doi.org/10.1016/j.still.2015.12.001

Zorn, M. I., Van Gestel, C. A. M., Morrien, E., Wagenaar, M., & Eijsackers, H. (2008). Flooding responses of three earthworm species, *Allolobophora chlorotica*, *Aporrectodea caliginosa* and *Lumbricus rubellus*, in a laboratory-controlled environment. *Soil Biology and Biochemistry*, *40*, 587–593. https://doi.org/10.1016/j.soilbio.2007.06.028